ASSEMBLING LIFE.

Models, the cell, and the reformations of biological science, 1920-1960

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I certify that all the intellectual contents of this thesis are of my own, unless otherwise stated.

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Abstract

The subject of this thesis are the fundamental, bioelectrical expressions of life from the interwar period into the 1950s. Or rather – at issue are very elusive manifestations of life – it is a history of *models* of the cellular life, and the things, materials and practices surrounding them.

This living cell, modelled or not, indeed is largely absent from the narratives we tell of twentieth century biology. The big pictures we have revolve around even smaller entities: genes, molecules, and enzymes. But the cell was still there, this thesis shows. And its presence, this thesis argues, must affect the stories of life science we tell. The historical material covered here thus deliberately encompasses a range of fairly obscure forays into the nature of bio-electricity – from exercise physiology to colloid science to medical physics - as well as such well-known advances as the Hodgkin-Huxley model of the neuron. For, the central aim of this thesis is to show that not only was this living cell central to shaping biological science in the twentieth century, we can uncover it at very mundane and unexpected places. Science, this thesis shows, knew the elusive cell mainly through other and mundane things – as models. These models were assembled from a fabric that was not living, organic and natural, but fabricated, processed, made-up and hence, known, controlled and transparent: things ranging from soap-films to electrical circuits to calculation machines.

It follows that this science of life was not in fact *life* science but something still broader which belongs to histories far beyond that of biological specialities, model-organisms, academic research and disciplines, or indeed, that of the progressive molecularization of life. Cellular life took shape – mediated via models – within broad-scale technological and scientific projects that coalesced around the macroscopic materialities that defined this modern, industrial age.

Sources and abbreviations

ADM	Records of the Admiralty, Naval Forces, Royal Marines, Coastguard, and related bodies, UK National Archives, Kew
AE	Personal papers of Sir Alfred Charles Glyn Egerton, Royal Society, London
AIR	Records created or inherited by the Air Ministry, the Royal Air Force, and related bodies, UK National Archives, Kew
AVHL	The papers of Professor A.V. Hill, Churchill Archives Centre, Churchill College, Cambridge
AVIA	Records created or inherited by the Ministry of Aviation and successors, the Air Registration Board, and related bodies, UK National Archives, Kew
BATES	The papers of John Bates (GCI/79), Wellcome Institute, Contemporary Medical Archives Centre, London
BBC	BBC Written Archives Centre, Reading
BL	Private papers of Sir Bernard Lovell, Imperial War Museum, London
BLRD	The papers of Sir Edward Bullard, Churchill Archives Centre, Churchill College, Cambridge
PB	Personal papers of Lord (P.M.S.) Blackett, Royal Society, London
BONHOEFFER	Nachlass Bonhoeffer, 16/6-8, Abt. III, Rep. 23, Archiv der Max-Planck-Gesellschaft, Berlin
CAB	Records of the Cabinet Office, UK National Archives, Kew
CHAFFEE	Personal papers of Emory Leon Chaffee, Harvard University Archives, Pusey Library, Cambridge, MA
CMB/64	Minutes of the Foulerton Research Committee and Medical Sciences Research Committee 1922-57, Royal Society, London
COLE/Columbia	Personal File, Kenneth S. Cole, Columbia Medical Center Archives and Special Collections, NYC
CUL/ULIB	Archives of Cambridge University Library, Cambridge
CUL/Min.V.68	Minutes of the Faculty Board of Biology 'B', 1931-1939,

	Cambridge University Library, Cambridge
CUL/Min.V.75	Minutes of the Professors; sub-committee of Faculty Board of Medicine, 1930-1935, Cambridge University Library, Cambridge
CUL/Min.VII.18	Minutes of meetings of the Natural Sciences Tripos Committee, 1932-1935, Cambridge University Library, Cambridge
DSIR	Records created or inherited by the Department of Scientific and Industrial Research, and of related bodies, UK National Archives, Kew
FD	Records created or inherited by the Medical Research Council, UK National Archives, Kew
FREMONT-SMITH	Personal papers of Frank Fremont-Smith, Countway Library of Medicine, Boston, MA
FORBES	Personal papers of Alexander Forbes, Countway Library of Medicine, Boston, MA
FRICKE/CSH	Hugo Fricke Collection, Cold Spring Harbor Library and Archives, Long Island
HD	Personal papers of Sir Henry Dale, Royal Society, London
HECHT	Selig Hecht Papers, Rare Book & Manuscript Library, Columbia University, NY
HDGKN	Personal papers of Sir Alan Hodgkin, Wren Library, Trinity College, Cambridge
HNKY	The papers of Lord Maurice Hankey, Churchill Archives Centre, Churchill College, Cambridge
LAB	Records of departments responsible for labour and employment matters and related bodies, UK National Archives, Kew
MC22	Personal papers of Norbert Wiener, MIT Special Collections and Archives, Cambridge, MA
MC154	Personal papers of Francis Schmitt, MIT Special Collections and Archives, Cambridge, MA
MCCULLOCH	Warren S. McCulloch Papers, American Philosophical Society Library, Philadelphia
MDA	Modern Domestic Records, Royal Society, London
NACHMANSOHN	David Nachmansohn Papers, Rare Book & Manuscript Library, Columbia University, NY
OSTERHOUT	Winthrop John Van Leuven Osterhout Papers, American Philosophical Society Library, Philadelphia

PRINGLE	Personal papers of John William Sutton Pringle, Bodleian Library, Oxford
RF/RG.1.1	Rockefeller Foundation Archives, PROJECTS, 1912-2000. Rockefeller Archives Center, Sleepy Hollow, NY
RF/RG.1.2	Rockefeller Foundation Archives, PROJECTS, 1912-2000. Rockefeller Archives Center, Sleepy Hollow, NY
RF/RG.303	Detlev W. Bronk papers, Rockefeller Archives Center, Sleepy Hollow, NY
RNDL	The papers of Sir John Randall, Churchill Archives Centre, Churchill College, Cambridge
ROUGHTON/APS	Francis Roughton Papers, American Philosophical Society Library, Philadelphia
ROUGHTON/CUL	The papers of Francis Roughton, Cambridge University Library, Cambridge
RI	Minutes of the Colloid and Biophysics Committee, Royal Society of Chemistry, Royal Institution, London
SCHEMINZKY	Personalakte Scheminzky, Med.12 Nr.4, Universitätsarchiv Wien, Vienna
T	Records created and inherited by HM Treasury, UK National Archives, Kew
UCC	Records Office, University College, London
UGC	Records created or inherited by the Higher Education Funding Council for England, UK National Archives, Kew
WILKINSON	Private papers of F. J. Wilkinson, Imperial War Museum, London
WO	Records created or inherited by the War Office, Armed Forces, Judge Advocate General, and related bodies, UK National Archives, Kew
YOUNG	Papers of John Z. Young, UCL Special Collections, London

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INTRODUCTION.

Assembling Life.

What am I, Life? a thing of watery salt, / Held in cohesion by unresting cells ...?[1]

Motto to Ralph Gerard's *Unresting Cells* (1940)
(from a poem (1917) by John Masefield)

De facto, it is relatively unimportant whether this or that theory is correct; instead, it is important to find a model made up of inanimate substances which produces the exact-same sort of electrical currents than a given specimen of excitable tissue.[2]

Richard Beutner, *Theorie oder Modellversuch?* (1923)

The cellular life, being little, is easily overlooked. Though always concerned with artificially extending their senses, it took scientific men well into the nineteenth century to ascertain it was there. Or this is how we tend to think of it: the cell, a product of the nineteenth century. The twentieth century, in turn, was about still smaller things: genes, molecules, proteins and enzymes.

The cell indeed is largely absent from the historical narratives we tell of twentieth century biology. And certainly enough, this unit of life, the biological cell, was no novelty in those days. The years 1938/39 marked the centenary of the *cell theory*.[3] Another centenary followed suit, passing 'almost unnoticed' in the midst of the war: that of the discovery of the action current of nerve and muscle – one of the fundamental expressions

1 See Gerard (1940).
2 Beutner (1923): p.571.
3 E.g. Aschoff, Küster, and Schmidt (1938).

of cellular life.[4] Regarding the cell, celebratory occasions were not scarce. The Germans revered Virchow, Pasteur for the French, Sherrington in England: cellular pathology, microbes, the synapse: vestiges of microscopy of the nineteenth century.[5] Cellular behaviour had long assumed a new dynamic life on celluloid - cinema screens - serving the popular, scientific edification.[6] It had turned into a topic for children's books: Robert Hooke, this 'curious man of the seventeenth century had no clue that with the word – cell – he created a name that would reverberate through the centuries to come: parole for science, revelation for pupils – oracle for the sage', read one of them, *Die Zelle* (1919): 'All life is cellular life'.[7]

In terms of the cellular life, the ensuing decades brought not so much novelty than expansion, diversification, and intensification. For students of the cell, like for everyone else, these modern times were, above all, dizzying, and moving fast: There was a 'gloomier side' to the rapid advances of knowledge as one English physiologist diagnosed in 1928: absence of 'common ground' and 'unifying principles', and (so he feared) 'abstracts of abstracts journals and reviews of reviews';[8] physiology suffered 'territorial losses', diagnosed another, biochemists claimed 'independence', zoologists 'jurisdiction below the level of the frog', anatomists left the 'dissection room to make experiments'.[9] By 1929, physiological science resembled 'une puissante *intelligence collective'* - 'une conquête faite par le modest savant de seconde classe (en réalité anonyme)'.[10] New specialities, new instruments, new journals amassed, and ever more rapidly.[11] As one observer gasped in 1947, within the last fifty years the 'insignia' of the physiological scientists had transformed from the

4 Hodgkin (1950): p.322.
5 On Virchow, see e.g. Cameron (1958); Reinisch (2007); on Pasteur, Bonazzi (1922); L. Ward (1994); on Sherrington, Sherrington (1947); Tansey (1997); R. Smith (2001a).
6 On the film/cell nexus, see Landecker (2004); Landecker (2005).
7 Kahn (1919): p.6; p.13.
8 Lovatt Evans (1928): p.290.
9 Adrian (1954): p.4.
10 Franklin (1938): p.307.
11 Physiology in the twentieth century is a very uncharted historical terrain. To get a sense of physiology's expansive developments, see Veith (ed.) (1954); Rothschuh and A. Schaefer (1955); Gerard (1958); Rothschuh and Risse (1973); Geison (1987); Sturdy (1989).

'microscope, smoked drum and inductorium, and a bottle of ammonium sulphate' into 'electron microscope, the cathode-ray tube, photo-electric-cell, manometric apparatus, and Geiger counter'.[12]

For the historians of the life sciences too, this period is one of deep transformation. Of more biology, more experimental biology, more quantitative biology, and of an ever intensifying, continuous 'borrowing from physics', as Garland Allen's *Life Science in the Twentieth Century* (1975) once put it.[13]

But the cell is absent from these narratives.[14] As if the cell never made it beyond the cell theory, and into the twentieth century. The big pictures that we have of this transformation have it written in their names: 'The Molecular Revolution in Biology', 'The Molecular Transformation of Twentieth-Century Biology' or 'From Physiology to Biochemistry'.[15] They revolve around smaller entities: the *molecularization* of life. And they revolve, as such, around the emergence of novel, academic disciplines: biochemistry, genetics, and molecular biology, in particular. They are narratives of the (cellular) life torn to bits and pieces. It is indeed easily overlooked how profoundly cellular life eluded science and remained intact, even in the twentieth century.

Big pictures, little cells, material models

The cell was there, this thesis shows. And its presence, I argue, must affect the stories we tell. In the twentieth century, although the historiography might seem to suggest otherwise, students of the cell turned legion, operating in and even more so, beyond academic

12 Lovatt Evans (1947).
13 Garland E. Allen (1975): esp. p. xix.
14 See esp. Kohler (1975); Kohler (1982); Abir-Am (1982); Fox-Keller (1990); Kohler (1991); Weatherall and Kamminga (1992); Kay (1993); Chadarevian and Kamminga (eds.) (1998); Hunter (2000); Kamminga (2003); Abir-Am (2006); Wilson and Lancelot (2008); Chadarevian and Rheinberger (eds.) (2009).
15 Morgan (1990a); Olby (1990); Abir-Am (2003).

laboratories: plant physiologists, general physiologists, biophysicists, colloid scientists, toxicologists and public health scientists, students of nutrition, food chemists, medical physicists, chemical physicists, industrial scientists, investigators of textiles, leathers, and fibres. The years 1925/1926 alone, for instance, saw the creation of three journals committed to the 'general' - and that meant the physico-chemical, cell-centred and ideally useful - physiology of plants: *Planta*, the *Journal of Plant Physiology,* and *Protoplasma.*[16] If this cell, the dynamic microcosm of life, was somewhat elusive - despite the rapid advances of knowledge, technique and science - this watery thing too turned pervasive, reverberating through the twentieth century. If not 'all life', much life then was 'cellular life'.

The aim of this thesis is to reinsert the cellular life into the big picture of biology's transformation in the twentieth century. Or more properly, its aim is to reinsert *models* of the cellular life and the mundane *materials* they were made up from and thus, the whole set of *their* histories. These materials - things ranging from soap-films to electrical circuits to calculation machines – here will serve to re-embed the cellular life within the historical landscapes of modernity that crucially shaped, I shall argue, the transformative incursions of physics into biology in particular.

These incursions, as we shall see, are a much belaboured topic among historians of twentieth century biology indeed. And they are, next to the fundamental problems of cellular behaviour – membrane permeability changes, energetic conversions and, as the thread I will follow most in this story, nervous action – the one theme that is running through the chapters to follow. But here these incursions will turn out to be no real incursions at all. They will emerge as something that was already integral to the mundane ways science knew cellular life: physics/biology are categories that did not suit the agents of the following story, the models and materials. These agents, they explode them.

[16] See nn. (1926a); nn. (1958); Hanson (1989).

Because, as I shall show, life's fundamental expressions have no history of their own. And neither has their source, the living cell – unit of life. The way science knew them was mainly through these other and mundane things - things that were less living, organic and natural, but fabricated, processed, man-made and thus, known, controlled and transparent. The real thing, for many a student of the cell, was palpable enough. But it was a substitute.

It follows that this science of life was not in fact *life science* but something still broader and disparate which belongs to histories far beyond and other than that of biological specialities, academic research and disciplines, or indeed, that of *natural* knowledge. These histories were the histories of making and knowing material, man-made things, scientifically. Cellular life, this thesis shows, took shape within the large-scale technological and scientific projects that coalesced around the mundane materialities that defined this modern, industrial age: the industrial analysis of complex, artificial and semi-synthetic materials and of produce and food stuffs; surface chemistry and the science of colloids; the applied physiology of athletic performance and industrial labour; the electrical, power and radio industries and an industrial scale, electronic war.

This was the complex world *known*. Useful, tested, analysed and understood (relatively much better), these mundane things, I shall argue, also generated a substitute fabric of life: synthetics and semi-synthetics, high-frequency radio waves and electrical circuitry, numbers, charts, plots and diagrams, and efficiently performing, muscular human bodies. The elusive, subtle nature of cellular life was *made up* – assembled - from this non-biological fabric: not simply from observation and experimentation, neither from words and theories but from the real, material and mundane stuff that populated scientists' life-worlds: Life's *ersatz*.

If the cellular life took shape mainly as its substitute this was not only because this unit of life, the microcosm of the cell, was largely inaccessible and perceived as such: beyond vision and intervention. It certainly was that, as we shall see. But more fundamentally, it was because of the ways knowledge production about the biological cell itself was anchored in the material, modern, and man-made world - apart from and beyond the sites that we tend to invoke when it comes to *life science* - laboratory, clinic, field, or museum.[17] This is where this thesis diverges from the existing literature.

The same will be true for the objects that mediated this knowledge. They already were, in a sense, essentially *bio-physical*, neither recognizably biological nor recognizably unbiological. This was a knowledge of *structures and processes* belonging to a world of industrial application rather than the university seminar. And the way science knew the living cell, I shall argue, was mainly through these fabricated things. Or more properly, it was through a whole spectrum of model-materials or what I call *ersatz-object*s.

The things that will figure in this history as cellular ersatz - soaps, surface films and electrical circuits, and more - embodied forms of mundane, scientific and technical knowledge in virtue of which they accrued model-function. Sometimes explicitly, as when students of cellular life deliberately appropriated these materials for modeling-purposes, say, 'market soaps' and their 'foaming properties' to replace what would have remained elusive otherwise: the dynamic behaviours of the cell surface.[18] And sometimes less explicitly: traversing the world, the spheres of fabricated things comprised in the following five chapters - synthetics, muscles, electrical circuits, numbers and electronics - shaped what there was to be known about things, their fundamental properties and processes, more generally: each sphere formed a kind of ontology of common and important things. They were mundane in this sense. But they were neither particularly natural nor emphatically un-natural.[19]

17 See esp. Cunningham and P. Williams (1992); Kohler (2002); Kraft and Alberti (2003); more generally, see Kohler (ed.) (2008); Ophir and Shapin (1991); Livingstone (2003).

18 More on this type of models in chapter 1. Cited is Fischer, Hooker, and McLaughlin (1921).

19 Similar kinds of arguments are more familiar from the history of the physical sciences. Telegraph, power and telephone networks, for instance, were crucial such non-natural objects of natural science. See esp. C.

Modeling by way of ersatz as is at issue in the following thus turns out to be a quite different matter than the models and models-creatures that have shaped our historical sense of models. It is, in fact, a very limited selection of exemplary items, representational technologies and allegedly radical developments that have shaped this sense: sticks-and-balls models of molecules, formal models, cybernetics and computational simulations, notably.[20] In their place, we will find modeling practices that were as unexceptional and mundane as were the material things they incorporated.

In the history of the life sciences, of course, it is model-*organisms* – such as, drosophila, mice, *C. elegans* and oenothera - that first come to mind. Half tool, half organism, but belonging quite unambiguously to the biomedical laboratory, these standardized, fabricated creatures also have deeply influenced the kind of narratives historians have come to tell about *life* science.[21] The material substitutes of the living cell, I shall argue, and the unnatural sciences of life *they* tell of, had little in common with them or with the similarly locally confined 'right tools' for the job.[22] Because these cell-models were deeply involved with the stuff of the world at large, the vanishing points of the present investigation were neither stabilization of local knowledge or research communities nor the trajectory towards homogenized science. And as *things*, they therefore had little in common with 'paper tools' either, these more abstract technologies historians of science have enrolled to ground even such seemingly disembodied enterprises as theoretical physics in practices.[23] These cell-models were, above all, fabricated things, a piece of cellophane foil for instance - concrete part of the world. Certainly, they did not respect the registers of

Smith and M. N. Wise (1989); Schaffer (1992); Hunt (1994); Mindell (2002); Schaffer (2004).

20 Of course, historians of science have long begun to explode the category 'model' into a myriad of different forms of modeling practice. Yet, these exemplary model-things have shaped historical analyses of models generally, both in terms of periodization and conceptualization. See esp. M. Morgan and Morrison (eds.) (1999); Cordeschi (2002); Wise (ed.) (2004); Chadarevian and Hopwood (eds.) (2004); Creager, Lunbeck, and Wise (eds.) (2007); Daston and Galison (2007).

21 See esp. Clarke and Fujimura (eds.) (1992); Kohler (1994); Creager (2002a); Rader (2004); on a critical note, see Geison and Laubichler (2001); and Logan (2002).

22 The 'local' is part of the programme, see esp. Clarke and Fujimura (eds.) (1992): esp. p.17.

23 See esp. M.J. Nye (2001); Klein (2001); Warwick (2003); Kaiser (2005); Jones-Imhotep (2008).

models belonging more properly to the philosophers of science: issues of formal structures, logic, semantics, epistemology, language, metaphor and representation.

The resulting picture of biological science is to prompt us to reconsider our intuitions about this period of transformation. In enrolling prefabricated knowledge rather than local standards, these mundane materials will lead us beyond these analytical units and philosophical registers - both, in terms of scientific models and (especially) in so far the biology/physics connexion is concerned. Significantly so: the 'incursion' theme provides the common reference point for much of what there has been written on biological science in the twentieth century, on its instruments, progresses and metamorphoses. Allen's turn-of-phrase, 'continuous borrowing' has been referred to already: his take was intellectual history, mechanistic materialism and vitalism the spectrum wherein which to locate actors.[24] Pauly's well-known account of Jacques Loeb who famously shaped a whole generation of American physiologists according to the 'engineering ideal' too revolves around the theme;[25] so did Abir-Am's influential work on the Cambridge 'Biotheoretical Gathering' and on 'colonization' by way of instruments and the Rockefeller Foundation in the 1930s;[26] not to mention the story of the post-WWII influx of disillusioned, war-weary nuclear physicists – the Delbrücks, Schroedingers, and Cricks - and the immense amount of commentary, critique and revisions this has drawn ever since.[27]

Yet these narratives, even the revisionist ones, tell a limited version of what biology was. Typically, they centre on the successive revolutions provoked by biochemistry, molecular biology and bioengineering (rather than, say, on the dissolution, fragmentation,

24 Garland E. Allen (1975); also see Roll-Hansen (1984); Lindner (2000); Fangerau (2009).
25 Pauly (1990); also see Pauly (2000).
26 Abir-Am (1987); also see Abir-Am (1984) and the responses (in the same issue); Kohler (1991); Kay (1993).
27 What we identify as molecular biology today, or this is perhaps the most striking aspect of the new, received picture, did not not exist for most of the twentieth century. What there was something called 'biophysics': it assembled a much more fragile, more scattered, more diverse set of forays into the borderlands of physics and biology than the usual suspects: proteins, genes, and molecules. See esp. Rasmussen (1997a); Rasmussen (1997b); Creager (2002a); Chadarevian (2002); Chadarevian and

and persistence - the *reformations* - of the physiological sciences). And typically, they centre on, or have been built around, a select number of themes, landmark events, and (academic) scenes: in the interwar period: Cambridge and progressive, leftist biochemists or the impact of the Rockefeller Foundation; the cold war, nuclear physics and DNA/genes; model-organisms, standardization, molecularization and the quasi-industrialisation of biomedical research.

Any one of these plots has been questioned, revised, twisted, and complicated. Indeed it is because of this that the incomparably more sophisticated and well-developed historiographies of molecular biology and biochemistry have shaped understandings of biological sciences in the period, generally.[28] When, consequently, the cell did make an appearance in historical accounts after all, it usually was in the form of a holist and/or anachronistic aberration, advanced by conservative scientists.[29] Relative to the institutional and disciplinary success stories of biochemistry and molecular biology, fractured and centre-less formations such as general physiology or colloid science - sciences centring on the cell rather than proteins and molecules – perhaps were neither particularly visible nor did they, or so we must assume, seem very respectable to those few historians who saw them – and dismissed them - as disciplinary 'failures'.[30]

There are, to be sure, exceptions to the pattern. But even these exceptions – the few existing historical treatments of the cellular life in the twentieth century - on closer inspection tell surprisingly familiar stories. Bechtel's largely philosophical *Discovering Cell Mechanisms: The Creation of Modern Cell Biology* (2006) is a version of molecular history: it is an account of an interdisciplinary merger between biochemistry and the biophysical art of

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Rheinberger (eds.) (2009).

28 For instance, the critical influence on interwar biology (and the origins of molecular biology in particular) that frequently is accorded to the Rockefeller Foundation almost exclusively has been spelt out in terms of fractions only of the Rockefeller Foundation: the 'vital processes' programme of its Natural Sciences Division. The equally extensive projects administered by its Medical Sciences Division, headed by neurophysiologist Alan Gregg, barely figure. See esp. Schneider (2002); Schneider (2007); also see Pressman (1998).

29 E.g. D. Smith and Nicolson (1989); N. Morgan (1990); Agutter, Malone, and Wheatley (2000); a notable exception is Hull (2007).

30 See esp. Kohler (1975); Kohler (1982); Servos (1982); Pauly (1987).

electron-microscopy in the 1940s and 1950s.[31] Also of fairly recent vintage and much more interesting, not least because it questions the kind of molecular vision that informs Bechtel's account, is Hannah Landecker's *Culturing Life* (2007). The book - its topic is in vitro tissue culture - like the present thesis, targets a history of the cell (not cell biology, the discipline) and the point of departure is indeed a similar one: despite the tremendous bias of the historiography towards genes and molecules, as Landecker observes (and shows), the cell has 'always been there', even before the coalescence of cell biology, that is.[32] The convergence may seem to go even further. Landecker's work, though branching out into quite different directions than the present study (such as, popular culture, film and cultural conceptions of time) treats in vitro cell cultures - 'living matter' - 'as technological matter'.[33] But like model-organisms, these cell cultures, as Landecker emphasises, were at home in the biological laboratory. They resided there from their inception in 1907 to their transformation into objects of industrial scale 'mass reproduction', 'standardization' and 'distribution'. As a 'technological matter', cell-cultures differ, evidently enough, significantly from the non-biological materials and sites that feature in the following. As a technological matter, these latter materials already existed in a distributed and mass reproduced form. And approaching the cell from these more literally technological substitutes for life, as we shall see, results in a significantly different historical picture.

We can, this thesis shows, tell different stories of *life* science. This is not only a history of cell models or certain cellular behaviours. It is meant to revise the big pictures we do have of the life sciences in this period – the interwar years and the immediate post-war decades - and of the big themes which have been worked into them. The picture that is

[31] Bechtel (2006); also see Bechtel (1993); Bechtel and Abrahamsen (2007).
[32] Landecker (2007): esp. pp.4-7.
[33] Ibid., p.2.

going to emerge here will be one less informed by disciplinary histories, narratives of scientific departure, and indeed, by common conceptions of what biological science was and where it happened. Instead, it will be one of the ongoing significance of the cell as an object structuring biological science; it will be characterised by continuity rather than profound incisions; and crucially, it will be one of biological - natural - knowledge production as inseparably intertwined with knowledge production about non-organic, man-made things – to the extent of effacing these disciplinary and ontological distinctions. The cellular life was, in a sense, mass-fabricated, all along.

Chapter 1, entitled **Semi-Synthetics**, is an account of the so-called 'permeability problem', a problem that, for its part, considerably occupied the minds of interwar students of the cell indeed: What was the nature of the cell surface, this all-important, fundamental boundary of life? The answers had everything to do with the artificiality of the world, as we shall see. Chapter 1 will fully introduce and develop the notion of modeling by way of ersatz-objects in the context of the burgeoning, industrial sciences of fabricated materials between the wars. Like the chapters to follow, it presents a way of construing the objects of the sciences of cellular life as fabricated, processed and mundane rather than simply *natural*. In this case, it was a true chemistry and physics of 'everyday life', as one observer noted in 1921.[34] They ranged from the analysis of semi-synthetics and plastics to studies of soaps, emulsions and foams to the biophysics of meat and produce. Models of the cellular life, as this chapter shows, were emergent from this scientifically penetrated, artificially prepared ontology.

Chapter 2 is on **Energy**, and it will examine another, fundamental feature of the cellular life: heat. It shows how the thermal manifestations and energetic conversions of the nerve cell took shape as part of a spectrum of investigations into the neuromuscular (human) body that began with muscle physiology and ended with industrial and exercise

[34] Bancroft (1921): p.2.

physiology. The substitutes at issue here were far less artificial, but they were equally mundane, fabricated and pervasive: the result of national efficiency craze, physical culture, healthism, and the contaminant, intense interest in athletic, labouring and efficient bodies in the interwar period, I shall argue, was a mundane ontology of energetic, muscular activity. And as this chapter shows, the elusive nerve cell turned into a little, athletic and efficient muscle as well – conceptually, materially, and technically.

The next chapter, **Circuits** leads back to cell surfaces - their transient, electrical changes, to be precise. And it leads on to another historical landscape: the 'radio age' and the wired, man-made, electrified world of the 1930s. At the time, excitable tissues, I shall argue here, quite literally turned into circuit components. There also emerged peculiar kinds of modeling practices which treated the electrical, transient behaviours of tissues by way of so-called 'equivalent circuits'. But nothing, significantly, was metaphoric here. These were models, this chapters shows, that formed concrete parts of a world which was populated by bioelectrical tinkerers who directed electrical currents to useful ends: they were devised to control, gauge, and analyse the effects of the electrical agent on biological materials - from whole patients to nerve membranes.

The final two chapters, called **Numbers** and **Electronics**, respectively, move onwards in time, into the 1940s and 1950s. Together, they trace a movement towards abstraction and towards the mathematical in matters of models of cellular, bioelectrical behaviour. But the point will very much be to anchor this movement in the materiality of concrete and worldly things. The resulting picture of this movement will differ significantly from existing ones. For, historically, certainly as far as models are concerned, the period is thought of as one of incisions and departures, in the first instance. The pictures we have centre, wrongly, I shall argue, on these incisions: on information theory, electronic brains, and notably, cybernetics, the models-science par excellence. This movement was, as these chapters show, partially one of displacements and partially one of concentrations in an abstract but nonetheless palpable medium of what went before. In the one case (chapter 4), this medium will revolve, notably, around mundane practices of computing; in the other case (chapter 5), it will form part of an expanding and equally mundane world of electronic gadgetry. Or that these practices and worlds became surprisingly mundane and banal, even for significant numbers of students of the cellular life, is what these chapters establish.

Each chapter, then, presents a kind of model practice, a particular incarnation of cellular life – the nerve impulse especially - and a set of material and historical conditions that shaped and mediated what the cell was, how it behaved and how it could be known. Together, they make a case for the cell – as the model-mediated object of a set of perhaps unfamiliar, certainly impurely biological, but significant forms of *life* sciences.

Important to this story will be a great many obscure and not particularly distinguished figures that themselves did not respect familiar historical categorizations: figures such as Ferdinand Scheminzky, a sort of biological radio-tinkerer with a background in high-tech mediumistic research, or Hugo Fricke, a trained engineer-turned-medical-physicist who knew as much about the electric resistance of breast tumours than about the thickness of a cell's membrane. Significantly, there will be very distinguished students of the cellular life as well, Nobel prize winners such as A.V. Hill and Alan Hodgkin, both products of the famous Cambridge School of Physiology – but they will not appear here in their capacity as products of this (or any) school.[35] Even the products of their researches, I show, are best understood as informed by the materiality of things. The real agents in the following will be the materials. It is in virtue of the kind of knowledge they embodied and generated that we will be able to understand the physico-chemical transformations in this period of biological knowing as a process that was both, pervasive and mundane.

[35] On the Cambridge School, see esp. Geison (1978); on 'research schools', see esp. C.M. Jackson (2006).

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The cell, then, was nothing absent in the twentieth century. Neither was it something new, nor, in fact, as historians such as Lenoir, Wise, Schmidgen and Mendelsohn have argued, was there in the nineteenth century a lack of cell models and representations, material and otherwise.[36] But when, in the following five chapters, we now turn to the model-mediated nature of the cellular life, it is not novelty that is at stake. In telling the story of the historical nature of cellular behaviour, the following moves very deliberately well beyond the laboratories or the narrow confines of academic physiology, and thus, the usual genealogies such as that of nerve behaviour which lead from Du Bois-Reymond onwards to Julius Bernstein, Keith Lucas, Lord Adrian, and eventually, to nervous messages, cybernetic signals and neural codes.[37] Telling the story for the twentieth century will make all the difference: It was not novelty but the synchronic, thick, material life-worlds that mediated knowledge of the cell, as we shall see.[38] Telegraphy and its well-known metaphoric interactions with the nervous system were new in the nineteenth century, but cells literally turned into circuits once electricity turned into a pervasive and common affair in the twentieth.[39] And much the same is true for the other things which will come to play their role: semi-synthetic and synthetic materials, or muscular activity and athletic subjects. Their roots too reach back deep into the nineteenth century. But they turned mass-ware much later. The difference was one of scale.

The following five chapters will indeed converge less with the recent surge of historical literature on models and model-organisms, but with the one on materials and their materiality. This literature is quite diverse, but like the work by Klein and Lefèvre on chemistry and its commercial objects, or Edgerton's on technologies *in-use*, in enrolling

36 Lenoir (1986); Brain and Wise (1994); Mendelsohn (2003); Schmidgen (2004).

37 On these genealogies, see Rothschuh (1959); Grundfest (1965); Rothschuh (1969); Lenoir (1986); Frank (1994); Bradley and Tansey (1996); Kay (2001); Piccolino (2003); Abraham (2003b); Piccinini (2004); Kandel (2006); Hagner (2006).

38 In this connection, this thesis is very much indebted to the arguments advanced in Edgerton (2006a); and Edgerton (2006b) chapter 8.

39 On the telegraphy metaphoric, see e.g. Otis (2002); Morus (2000).

them into this story of models the following is interested, in the first instance, in making this account less academia-centred, less discourse-centred, and thus, arguably, more historical as well.[40] Each of the following five chapters will raise more specific points in this connection. In investigating the cell and its material models, these chapters will scrutinize the historiography of scientific modeling, the history of neuroscience, and notions such as 'interdisciplinary' too - it is not only the molecule which obscured the cell from historical vision. For instance, the disproportionate prominence of the central nervous system in the historiography of the neurosciences - the seductive 'romance of the brain' as one perceptive historian has labelled it (albeit without much effect)[41] - had much the same effect when it comes to the nerve cell. This was a less romantic but much more accessible thing whose behaviours, as mentioned, will figure quite prominently in the chapters to follow. 'Neuroscience' will be a sub-plot at best in the following, but that the nerve cell was 'there' amidst mundane things - artificial materials, the phenomena of athletic performance, and high-frequency radio waves and its medical uses – also means to uncover, I shall argue, a history of nervous behaviour at very unexpected, unromantic places. This history had little to do with the brain, let alone, the mind.

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40 On materials, see esp. Appadurai (1986); Mendelsohn (2003); Edgerton (2006a); Rentetzi (2007); Klein and Lefèvre (2007); Daston (ed.) (2007); Alder (ed.) (2007); Trentmann (2009); Klein and Spary (eds.) (forthcoming).

41 Cozzens (1997): p.156; also see Braslow (1997); examples for the generally mind/brain-centred historiography of the neurosciences prominently include Harrington (1987); Satzinger (1998); Pressman (1998); Hagner and Borck (eds.) (2001); Hagner (2004); Borck (2005).

(1) SEMI-SYNTHETICS.

The artificial nature of the cell membrane

> *Today it is hardly doubtful that the permeability problem rests at the centre of attention of all those biologists who contribute to the creation of a physical chemistry of the cell.*[42]

'A measured amount (5 cc.) of a viscid gelatine (2 grams in 100 cc. Water) was gently stirred together with an equal volume of distilled water or an equal volume of m/500 silver nitrate. The appearance of five tubes forty-eight hours after being thus prepared is shown in the upper row of Fig. 111':

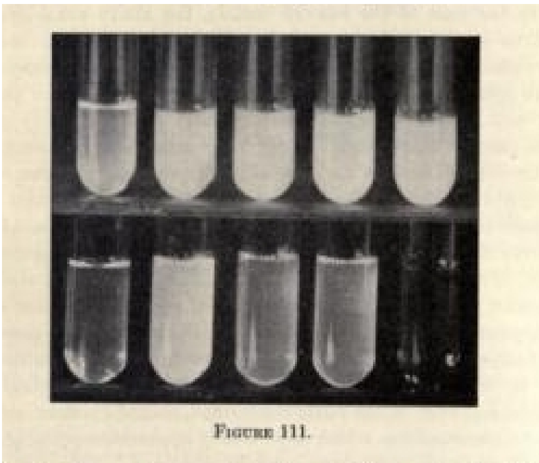

Figure 1: reversal effects, 1921

'There was now added to these tubes ... 5 cc. Water, 5 cc. m/3 sodium sulphate, 5 cc. m/10 potassium hydroxide. The lower row of Fig. 111 shows the effects of such treatment thirty six hours later.'[43]

'Lest it be thought that these observations on "dead" proteins do not apply to the "living" tissues', Martin Fischer, Professor of Physiology at Cincinnati, and author of *Soaps and Proteins: Their Colloid Chemistry in Theory and Practice,* supplied observations on

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[42] Gellhorn (1929): p.viii.

[43] Fischer, Hooker, and McLaughlin (1921): pp.237-238.

'reversing effects'. Thirty-six hours later, such effects - the result of mixing salts into these gelatine systems - were clearly visible (certainly in the photographic evidence supplied in Fig. 111).

The year is 1921, and Fischer just about in the midst of a priority dispute with George Clowes, the director of research at the Eli Lilly Company. At stake is the nature of the cell - the unit of life – or more properly, the nature of the cellular surface. Clowes himself, until recently on the staff of the US Chemical Warfare Service, had made a reputation for having succeeded to *duplicate* - in 'purely physical systems' - the disturbing effects of negative ions (and the 'protective' action of positive ions) on certain biological systems.[44] Clowes too had studied certain reversal effects in oil-water emulsions; their dependence, that was, on the presence of emulsifying agents – soaps. And like Fischer, Clowes was intrigued by the 'resemblance' of such soap-emulsions to cellular behaviour. Here one was able to 'secure', as he said, 'insights into the exact nature' of the cell's surface.[45] Soaps promoted the formation of membranes, and the relative solubility of these membranes determined the type of the resulting emulsion: oil-drops dispersed in water 'like in cream', Clowes said, or alternatively, water in oil 'like butter': [46]

[44] Clowes (1916b): p.753; and e.g. A.W. Thomas (1920).
[45] Clowes (1916b): p.754 .
[46] Clowes (1916a): p. 421.

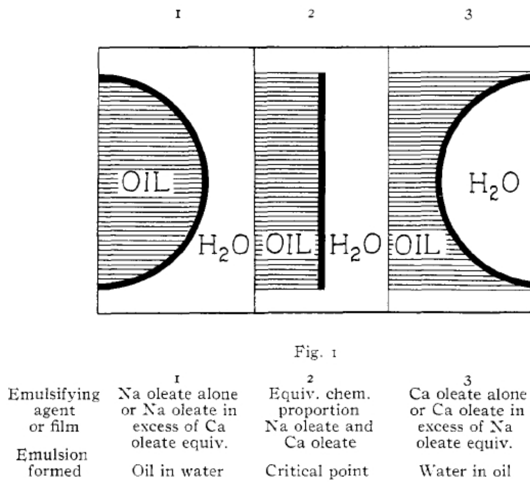

Figure 2: emulsion reversal, 1916

This was biophysical modeling, interwar-style, in action. Such behaviour deeply resembled alterations of cellular permeability, as Clowes detailed. Fischer, for his part an expert on oedema, was naturally interested in the effects of salts on tissues and he too had found 'surer ground' in soaps - by virtue of their 'more controllable number of purely chemical variables'.[47]

When it came to knowing the cell, everything was a question of controllable, knowable substitutions. Fischer and Clowes clashed over the question, then, of who had first approached the exact nature of the cell by way of detour through emulsions.[48] Equally at stake were, on the one hand, such 'technical problems' as were 'embraced in the making of butter'.[49] And on the other, a new theory of the cell membrane. It became known as the emulsion-reversal theory.

Here was a theory of the cell fabricated from man-made materials: soaps and emulsions. There were others: Like Clowes and Fischer, students of cellular permeability in this period, this chapter shows, routinely fabricated their science out of a rapidly modernizing world of processed materials: a world more or less synthetic, made up complex stuff, and importantly, as we shall see, teeming with palpable *surfaces*: a world of

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47 Fischer, Hooker, and McLaughlin (1921): preface., and p. 205 .
48 see esp. Fischer (1918): p.195.
49 Fischer and Hooker (1916): p. 468.

soaps, emulsions, plastics, lacquers, foils and foams, of margarine, milk, and gelatine. Intersecting with these developing physiological conundrums, the 'combined effect' of intense research efforts in colloid science and physical chemistry had been, as the physical chemist Sir Fredrick Donnan diagnosed in 1926, 'to reveal the existence of a newly recognised so-called "two dimensional" molecular world'.[50]

Exploring these landscapes will naturally lead us into the sort of material history of the cell that is the subject of this thesis. Here in particular it will naturally lead us to the notion of models as ersatz-objects, as appropriations of the everyday and ready-made. Actors called them model-experiments, artificial models, imitations, and *Modellversuche*.

The landscapes this chapter enrols in the picture will be broadly familiar ones: it are the vast interwar worlds of new, and newly colourful and plenty synthetic and semi-synthetic stuff, created, for the most, by the chemical industries; the era of DuPont and IG Farben, of dreams of national autarky and a chemically engineered, man-made world. These *masses* of artificial creations, recreations and substitutions of nature, and the ontological confusions they provoked - amplified by such novelties as photography – were rooted in the nineteenth century, as notably Orvell's *The Real Thing* has argued. Between the wars, these ever-diversifying objects and materials turned increasingly mundane, embraced as a reality in themselves, rather than something *merely* artificial and second-best. Substituting and processing nature, whether fuels, rubber, textile fibres, or butter, were large-scale, economic and technologies projects.[51] Everywhere one looked, science journalist John Pfeiffer wrote in 1939, one saw the 'moldable rivals of metal, lumber, china, and such materials that go into the making of objects for your home and office, [they] are all around you in various forms'.[52]

These mundane materials - useful, analysed, tested, and processed - and the

50 See preface to Rideal (1926).

51 The literature is large, but scattered; see esp. Hounshell and J.K. Smith (1988); Orvell (1989); Meikle (1995); Mossman (ed.) (1997); Furukawa (1998); Heim (2003); Westermann (2007).

52 Pfeiffer (1939): p.54.

knowledge produced in the process, also went into the making of cell-models, as we shall see, both explicitly, and implicitly. The resulting picture of the cell will be an unfamiliar one. Recovering the material dimensions of model experimentation will mean to think very differently about a period and developments that historiographically have been framed in terms of an incipient molecularization of the living, or as a matter of intellectual and philosophical programmes – think of Loeb's 'engineering ideal' or the leftist-progressive 'outsider' politics of Cambridge biologists and the influential accounts thereof, by Pauly and Abir-Am, respectively.[53] There *will* be simplification and reduction of life's complexity – but this too was already 'all around you in various forms'. In what follows, it is the materiality of fabricated things, and the mundane knowledge embodied therein, that is of central importance. The incursions of physics into biology will emerge as one epiphenomenon of the broad-scale, scientific penetration of everyday, synthetic things and materials.

Theories of the nature of the cellular surface were largely based, as we shall see, not on observations, not even mere experimental interventions, but on concrete manufacture: a certain number of 'controllable variables'. More specifically, then, this chapter presents an account of what emerged, in the period between the wars among students of the cell as the so-called 'permeability problem'.[54] And this, crucially, was no minor problematic. The nature of the membrane, and the maintenance of selective permeability in particular - the fact that cellular surfaces excluded certain substances (and not others) – unquestionably belonged to the fundamental criteria of life. Bioelectrical phenomena but also nutrition and drug action in some way or another all would depend on certain fundamental principles governing the movement of substances across cellular surfaces. But the cell, and even more so, its putative composition were widely perceived as beyond vision and intervention.

[53] On Loeb, see Pauly (1990); on outsiders, see Abir-Am (1987).

[54] E.g. Osterhout (1924); Stiles (1924); D. Landsborough Thomson (1928); Gellhorn (1929); Höber (1932).

Part I of this chapter is concerned with the manifold, model-based approaches to the problem and its contexts: the development of a veritable culture of mimetic experimentation amidst the unfolding sciences of everyday surfaces. Part II will be concerned with what is perhaps the best-known and iconic advance in the physiology of cells then in the making: The so-called bi-molecular layer model of the cell membrane. And, one of the main upshots of this chapter will be, it squarely belonged - despite its apparent molecular sophistication, and despite its unquestionable academic nature – to a world of products, common things, and useful materials.

Things that matter

From Fischer's vials, jump forward a few years. Cambridge, Lent term 1931: a small group of advanced students of physiology in a class-room at a safe distance from industrial, modern life. The lecturer: Francis Roughton, reader in the Physico-Chemical Aspects of Biology. His topic: the Physical Chemistry of the Cell. This meant 'surface phenomena': 'when you have excluded all such processes from physiology', he challenges his students, 'it may well be asked "What is left?"'[55]

Not much. Surfaces, after all, as Roughton had surmised elsewhere, were a 'subject which bulk[ed] largely on the mind of the physical chemist of to-day'. Roughton himself, of course, had in mind especially the 'Borderland of Physical Chemistry and Physiology'.[56] This was very much a borderland of substances and material things, more or less unnatural ones: the world of the Seifrizs and Clowes rather than pure biological science. And even Roughton's Cambridge students were exposed to the cell as the swelling of cellulose, gels, films, emulsions, or soaps - materials 'studied intensively', though usually not, as Roughton explained, 'through a biochemical call'.[57] Lectures VI-VII, in particular, dealt with the 'new

[55] 'Lectures Lent Term 1931', Box 34. 10; 'Surface Phenomena IV', ROUGHTON/APS, Box 34.40u
[56] Roughton (1927): p.870 .
[57] 'Surface Phenomena VI', ROUGHTON/APS, Box 34.40u

work' on soap solutions; the course as a whole lead the student from surface tension, via adsorption, to molecular orientation in thin films, emulsions and eventually, permeability and gel structure. It was a 'difficult task of applying this information to [the] exceedingly fundamental question' of cellular permeability.[58]

Clowes' life-modeling via investigation into soaps and reversals was no isolated case, as Roughton laid it out for his students. There were also the explorations of soaps by James McBain, for instance, until recently, Professor of Chemistry at Bristol, and by figures such as Emil Hatschek of London. Hatschek was the author of the *Introduction to the Physics and Chemistry of Colloids* (1913) and instigator, at the Sir John Cass Technical Institute in Whitechapel in 1911, of the first regular course in colloid chemistry on English territory.[59] Running to its fourth edition by 1922 and covering topics from the latent photographic image to biological swelling, Hatschek's *Introduction* was 'strongly recommended for use in unusually wide circles'. It would 'even be of great use in schools', one reviewer opined, 'as bringing the scientific courses into much more direct contact with our knowledge of the materials of daily life and industry'.[60]

Such direct contact with the materials of daily life was the power and the strength of the new science of colloids and surfaces. Colloid, physical, electro - and surface chemistry grew rapidly during the early decades of the twentieth century, and in close affinity to simultaneously expanding industries. Connected with such names as Langmuir, Nernst, Haber and others, the entrepreneurial, object-based nature of even a science such as physical chemistry is well known.[61] Ranging from incandescent lamps to galvanic cells, here was one of the many origins of this new surface world, a world replete with membranes, boundary potentials, phases.

It deeply impressed physiologists everywhere, busy appropriating the new wisdom

58 'Surface Phenomena IV', ROUGHTON/APS, Box 34.40u
59 nn. (1944): p.7.
60 nn. (1920): p.226.
61 G. Wise (1983); Servos (1990); Lenoir (1997); Barkan (1999).

of physical chemistry. 'Some authors even wr[o]te of an epoch', as one such cell-modeller surmised in 1923, 'of physical chemistry in biology'.[62] The 'bible' of interwar physiology, *The Principles of General Physiology* (1914) penned by UCL physiologist William Bayliss, presented such influx in concentrated form. It was a challenging exposition of life from 'viewed from the physical and chemical standpoint'.[63] Then, or so Joseph Barcroft, Cambridge Professor of Physiology, judged in 1926, to 'the body of the younger men, … the book was in the nature of a revelation.'[64] A fourth edition had been in the making by 1924, struggling to keep pace with the rapid advances: 23 chapters guided the reader through the 'essentially dynamic' processes of life.[65] Surfaces loomed large.

Not only in physiology: In their hey-day, the 1920s and early 1930s, emulsions, jellies, sols, films, and filaments, and the phenomena of swelling, adsorption, mixing, and stability came together under the rubric and umbrella of the colloidal state of matter. Here, a new science of colloids was in the making, which was even closer in contact with the things. Though frequently traced back to the dialysis experiments of the British chemist Thomas Graham in the 1850s and 60s, colloids received their major boost during and in the wake of the Great War.[66] Colloids, or colloidal systems, technically a type of mixture consisting of two phases (a dispersed phase, and a dispersion medium), were anything that was not 'simple': smoke, foams, cream, mayonnaise, gelatine, agar were prototypical examples. From explosives to the photographic industry to margarine and the protoplasm, the objects of this universal science constituted the realm of a veritable science of complexity avant-la-lettre.

From a theoretical point of view, the excitement owed much to the recent investigations into surfaces. Technically, it owed to recent developments in laboratory technique, notably the ultra-microscope, ultra-filters, and ultra-centrifuges - all of which

62 Beutner (1923): p.571.
63 Bayliss (1924): pp.xv-xvi; pp.37-40.
64 Barcroft (1926): p.xxx.
65 See Foreword to the fourth edition, Bayliss (1924).
66 Esp. Ede (2007); also see Servos (1982); also see N. Morgan (1990).

made their appearance during the early decades of the century, and being 'ultra', resolved things into hitherto neglected dimensions.[67] And it simply owed to the surge of investigations into everyday, and thus non-simple, and thus presumably colloidal objects. As Charles Cross, British inventor of *viscose*, wrote in 1926, in terms of their industrial importance, the 'fine' chemical industries - the 'manufacturers which produce chemical individuals fully identified as such in the text books' – paled in comparison. They were to be set against the 'complex colloids': 'the industries based on vegetable and animal products and minerals used as such - textiles, paper making, rope and twine, leather, building construction ... paints and varnishes, glass, porcelain and earthenware, india rubber, military explosives, starch gum, gelatine and casein ... coal and foodstuffs.' The 'outstanding characteristic' of the times, he continued, was the 'recognition' of the less simple forms of matter as a legitimate scientific object.[68]

As these emergent sciences of materials began to uncover the ubiquity and omnipresence of surfaces and surface-processes in the world, it was the very ontological porosity of *surfaces* that enabled the smooth migration of concepts and materials – as models, imitations, ersatz-objects - in these borderlands of the living and non-living. Fischer and Clowes indeed were not the only ones who entangled surfaces, cells, models, and common things. Rather, they were practising, as will become clearer in due course, what was normal science: a 'borderland' only through the lens of academic classifications.

Especially colloid science eludes any such categorizations. Colloids were all about non-disciplinary inquiry. They constituted a productive site of intersections where objects, techniques and concepts were produced, analysed and trafficked. Colloid science would concern this *World of Neglected Dimensions* as Wolfgang Ostwald's catchy-titled manifesto of 1914 had it - not the simple, pure, and purified but the complex and real world. An English translation, thanks to Fischer above, hit the bookshelves by 1917. Son of the physical

[67] More on filters below - also see, Ede (1996); Bigg (2008): pp.316-319.
[68] C.F. Cross (1926): p.viii.

chemist Wilhelm Ostwald, sometime collaborator of Jacques Loeb, Ostwald would turn into one of the most vocal propagandists of these neglected dimensions. He was instrumental when in 1922, supported by firms such as *Continental-Cautchouc*, *Carl-Zeiss* and the *Electro-Osmose A.G. Berlin*, a German Kolloid-Gesellschaft was launched.[69]

Ostwald's address - 'Why found a Society?' - read like a piece in the sociology of science: a society would serve as a crucial platform for fund-raising and promoting 'public recognition', he declared. Indeed, perhaps never before had the need been felt so urgently than in the case of this 'young science': it cut 'across the domains of so many other disciplines' that without a society any single individual would have to be put into the 'state of a high-frequency oscillator' to keep pace.[70] Colloids, though of national importance, were nothing confined to nations. In the US, the case was pushed forward by the National Research Council, which spun off its own Colloid Committee in 1919. In 1924, as the *Time Magazine* reported, plans for a 1.000.000 US$ National Institute 'devoted solely to tracking down and getting acquainted with the elusive colloid' thus were well underway (though never realized): colloid science, one read, now played a 'leading role in biology, agriculture and hundreds of industries'.[71] Liverpool chemist William Clayton, author of *Margarine* (1920), approvingly welcomed the post-war surge of practical laboratory manuals in particular. They would, as he wrote in 1923, hopefully meet the 'much-needed want in teaching students the practical side' of the subject.[72]

In England, the BAAS had formed a Committee on Colloid Chemistry still during the war. True to the colloidal spirit, its reports - reprints being issued owing to 'continued demand' by the newly created Department of Scientific and Industrial Research - covered an immense range of 'processes and applications' stretching from tanning, rubber, nitrocellulose explosives to physiological subjects.[73] The Committee was chaired by

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[69] nn. (1922); also see Sühnel (1989).
[70] Ostwald (1922): pp.354-356.
[71] nn. (1924).
[72] Clayton (1923): pp.49-50; and see Clayton (1920); Clayton (1932).
[73] See preface to BAAS (1917).

Frederick Donnan, then in the 'thick of scientific and technological battle' designing production plants for explosives and mustard gas for Brunner Mond & Co. Its express purpose was to promote 'vigorous prosecution of scientific research'.[74]

The Committee therefore co-opted 'experts' such as Clayton, Hatschek, Bayliss - soon to publish his *The colloidal state in its medical and physiological aspects* (1923) – as well as Cambridge colloid scientist William Bate Hardy, Hardy's protégé Eric Rideal and Henry Procter, formerly professor of applied chemistry at Leeds and 'acclaimed on every side as the pioneer of a scientific leather industry'.[75] This colourful lot of experts converged, in Hardy's phrasing, on the 'boundary states' of matter. Hardy himself (more on whom later), Rideal will write, at the time realised 'that his explorations were leading him into contact with others who were not primarily biologists, but who were occupied with problems similar in many ways'.[76]

Trained as a zoologist in the 1880s and 1890s at Cambridge, Hardy had been led, via histological work, to the colloidal phenomena of coagulation and adhesion, and eventually to studies of lubrication, films of fluid, and their composition and stability. Hardy was widely perceived at the time as having originated, 'from an entirely different viewpoint' than Langmuir at General Electric, investigations of molecular orientation in surface films, or as Hardy, put it, 'the boundary state'.[77] 'It was to the genius of W.B. Hardy', surface enthusiast Rudolph Peters, himself a Cambridge Physiology product, wrote in 1930, 'that we owe the first experimental evidence that surface structure in the chemical sense exists.'[78] Other credited Hardy with so having spawned one of the 'most significant branches of Biophysics'.[79] 'Hardy's field' in fact was not easily labelled and ranged, in typical colloidal fashion, widely: work in the 'borderline field between biochemistry, physics,

74 Ibid., p.1.
75 nn. (1929): p.i .
76 Preface to Hardy (1936); F.G.H. and F.E.S. (1934); more generally, see N. Morgan (1990).
77 Gortner (1936): p.857.
78 Peters (1930): p. 779.
79 Roughton, 'History of Biophysics in Cambridge', p.1, ROUGHTON/CUL, B.31

colloid chemistry, and physiology' which Hardy most actively fostered.[80]

Hardy embodied the sort of not-easily classifiable, application-minded producers of biological knowledge that will figure prominently in the following. And they would, as we shall see in the course of this chapter, exert a significant influence on the ways biological sciences was pursued - not least, in Britain. Notably chairman Donnan himself was busy advancing the science of surfaces. While designing explosives production processes, Donnan even had found time to muse profoundly about 'La science physico-chimique' – 'Décrit-elle d'une façon adéquate les phénomènes biologiques?' he asked in 1918.[81] Donnan, while he would acquire something of a reputation for his bio-philosophical musings, very concretely came to endorse work of this borderline type at his future UCL Chemistry Department, which he turned into a flourishing centre of physical chemistry and chemical engineering.[82]

It was one of the many sites where the sciences of materials, of processes, surfaces and cells intersected. Figures such as future biophysics impresario Francis Schmitt would return to America convinced that 'obviously ... the electric properties of thin films [were] extremely suggestive to nerve physiologist'.[83] From the less sublime borderland projects, for instance, on 'Colloids in Sewage' (on behalf of the DSIR Water Pollution Research Board) to the work that eventually lead to the bi-layer model of the cell membrane, Donnan, a Rockefeller officer approvingly noted, was 'anxious' to get physico-chemistry into closer touch with the biologists.[84]

Like many another, Donnan was then gradually being lead into the 'realm of living processes' by a 'mixture of thermodynamics and colloid chemistry'.[85] In his case, this was

80 Gortner (1936); nn. (1934b); nn. (1934c).
81 Donnan (1918).
82 Divall (1994): p.262; Roberts (1997): esp. pp.301-304.
83 Schmitt, 'The physical nature of the nerve impulse' (c.1932), MC 154, Box 3, Folder 7; on Schmitt, see Rasmussen (1997a).
84 Minutes of the Water Pollution Research Board, 9 July 1929; 'Interview with Donnan', DSIR 13/58; Gerard, 'Miscellaneous Notes from London and Plymouth' (1934), RF/RG.1.1, 700 A, Box 18, Folder 131
85 Donnan (1932): p.167.

due, mostly, to Donnan's own, and hugely important theory of membrane equilibria: it dealt with the analysis of ionic equilibrium conditions and potentials at a semi-permeable membrane. Devised during the early 1910s on the basis of parchment paper and congo-red, the 'Donnan equilibria' found applications almost anywhere where surfaces were important: this meant almost anywhere – from cellular permeability to the manufacture of leather - as was persuasively demonstrated by one of Donnan's numerous disciples, Thomas Bolam, in *The Donnan Equilibria and their application to chemical, physiological and technical processes* (1932).[86]

Like Hardy's work on surfaces, Donnan's membrane theory was appropriated widely. And like Hardy's work, it emerged as a focal point of conceptual and material exchange, provoking and enabling the conflation of surfaces, materials, and ersatz-objects; and so did the many, and typically more 'indefinite concepts in colloid science', as a DuPont chemist observed in 1931 at a lecture at King's College of the same title - adsorption, equilibria, diffusion, films, micelles, viscosity, to name a few. They typically dealt with a diversity of materials in 'transition states' and of 'intermediate nature', and a wealth of apparently unrelated phenomena: a less-than-ideal world.[87]

The similarity of problems that was being exposed here accordingly operated in the midst of real things, on the concrete level of materials, practices and technique rather than in the abstract. Trivial as it may sound, it is important to emphasize this point: first because this was, of course, what intimately entangled cellular nature and synthetic substance; and second, because historians typically have derided colloid science a little more than an obscure episode: 'A Disciplinary Program That Failed', in John Servos' words, and for historians of biochemistry in particular the period went down as a 'dark age of biocolloidity'. But to focus on the academic and theoretical debates that were indeed

[86] Bolam (1932); and Loeb (1922).
[87] Cofman (1933): esp. pp.143-144.

fiercely being waged is to miss the point.[88] At stake in colloids, generally, was no academic discipline but the fabrication of complex things, and for the majority of scientists this meant a domain of everyday processes, structures and materials: the complexity of colloidal *behaviour* as opposed to an independent realm of laws.[89]

There was no dark age. The success of the chemistry and physics of everyday materials in Britain alone is indicated, for example, by the wealth of research associations that were created in the wake of the war as an adjunct to the DSIR. These were hardly pushing a disciplinary programme. All, however, were concerned with more rather than less complex things. A far from exhaustive list would include: Paint, Lacquer, and Varnish; Coal and Tar; Cotton Industry; the Launderers' Research Association; Rubber and Tyre Manufacture; the Flour Millers' Research Association; Cocoa, Chocolate, Sugar, Confectionary and Jam Trade; the Research Association of the British Food Manufacturers. Instruments devised to promote the pooling of resources for the purposes of 'fundamental' research - among industrial firms - into processes and products, sharing problems and phenomena across domains here was programmatic.[90] The Fabrics Co-ordinating Research Committee, for instance, established in 1921 explicitly recognized this fact. It was set up - in the 'cooperative spirit' - to avoid duplication and wasted efforts.[91]

The knowledge and materials that were being generated here, we will see worked into cellular life. In the same year, 1921, Jacques Loeb, in his contribution to a meeting in London on The Physics and Chemistry of Colloids, announced that Donnan's 'ingenious theory of equilibria' had made possible the development of a 'quantitative theory of colloidal behaviour'.[92] Loeb's own influential work on the colloidal behaviour of proteins itself had been heavily inspired by a recent 'theory of vegetable tanning'. Proposed by

88 Servos (1982); the 'dark age' phrase comes from Florkin (1972); also see Kohler (1975).
89 On this distinction, see e.g. Bogue (ed.) (1924): esp. v-vi.
90 Esp. Edgerton and Horrocks (1994); S. Clarke (2009).
91 See preface to HMSO (1925).
92 See Appendix 1 to HMSO (1921); preface to Loeb (1922); also see Pauly (1990): esp. pp.150-160; Fangerau (2009).

Procter above, it was the first application of Donnan's work to organic systems. Author of a *Leather Industries Laboratory Book* (1908) and *The Making of Leather* (1914), Proctor, in order to elucidate the 'fundamental action' of the tanning process then had turned to simpler systems and studied the action of electrolytes on gelatine swelling. In a more accessible manner than hide fibre, Procter found, gelatine jelly formed an 'ionisable salt of collagen'.[93]

This made applicable the Donnan membrane theory, and it lead Procter to believe that such systems were not 'simple' 'emulsions'. They were 'sponge-like structures, containing ... microscopic pores'.[94] Even if, as the critics intervened, conclusions based on such manoeuvres were 'somewhat over-emphatic', as strictly, theories such as Donnan's were applicable to ideal solutions only, in the real world, it productively generated series of substitutions:[95] Leather, hides, soaps, gelatine, protoplasmic surfaces, parchment paper - problems similar. There was now a 'consensus of opinion' emerging regarding the colloidal behaviour of soaps, gelatine and similar such materials, as Wilhelm Seifriz of the Yale Botanical Laboratory, reported in 1923. Seifriz himself had just recently returned from the Kaiser-Wilhelms-Institute for Physical Chemistry, Berlin, its new Division of Colloid Chemistry and Applied Physical Chemistry to be precise. For Seifriz, such consensus implied that in the protoplasmic surface too, 'there [was] no reversal of phases in the formation of a gel, but merely an aggregation of the colloidal particles'.[96] This was bad news for Clowes' emulsion-reversal theory of the cell, and still more devastating evidence for the absence of reversals Seifriz supplied himself - with the 'courteous cooperation' of the Research Laboratories of Standard Oil and model-experiments with Perfection Water White kerosene, Diamond Paraffin Oil, and 2900 Red Oil. This allowed for an especially controlled attack on emulsions - all oils being high-grade and their physical characteristics – specific gravity, boiling range, molecular weight - well established.[97]

93 Procter (1916): p.1330.
94 Procter (1921): p.40.
95 A.V. Hill (1923): p.695.
96 Seifriz (1923): p.695.
97 Seifriz (1925); on Seifriz, see nn. (1956).

The reality-effects of cellular ersatz operated, evidently, on many levels. Procter's hides grounded them as much as the more explicitly cell-directed model-experiments of a Seifriz or Clowes. And there was system to such substitutions, as this section has shown. In Britain, the scene to which we will return when we investigate the genesis of the bi-layer model, the most formal, and certainly the most visible platform for the mutual interpenetration of things, physics, and biology were the activities of the BAAS Colloid Committee and its successor, the Colloid Committee of the Faraday Society. It was launched in 1928 - on Hardy's initiative.[98] Its first action was to organize a conference on 'Colloid Science Applied to Biology' which was held in Oxford in 1930. With an impressive line-up, it attracted some 250 participants.[99] The Colloid Aspect of Textile Materials (1932), Colloidal Electrolytes (1934), or The Properties and Functions of Membranes, Natural and Artificial (1937) belonged to the notable future meetings, and among the active, roughly a dozen committee-members, Hardy and Donnan's circles dominated. They made up 'a truly great ~~team~~ band', as Roughton later scribbled in his notes.[100] And as we shall see, in the surface world they helped create took shape, as a form of ersatz-knowledge, a lasting vision of cellular nature. But to see this, let us first more fully explore its basis: a vast culture of cellular ersatz-modeling.

Mimetic culture

This section and the next consider in more detail what emerged between the wars as the definite vision of the cell and its reliance on modeling by way of ersatz. They came together in the so-called permeability problem and thus: surfaces. The emulsion-reversal theory provided one example, but, as we shall see now, it formed part of a much broader

[98] Minutes of the Colloid Committee, esp. 5 June 1931, RI; also see Rideal (1953).
[99] Minutes of the Colloid Committee, esp. meetings 24 October 1934; 18 September 1936, RI; Roughton, 'History of Biophysics in Cambridge', p.2, ROUGHTON/CUL, B.31; Butler (1953).
[100] Roughton, 'History of Biophysics in Cambridge', p.1, ROUGHTON/CUL, B.31

process of enmeshing life and artifice which was driven by the materiality of models themselves. The materials in question weren't simply materials, as we already have seen, but useful ones, made transparent by science, and as such, furnishing interwar lifeworlds. The Proctors, Hardys, and Fischers, in turn, practised a form of biological science that does not neatly fit the usual philosophical categorizations historians brought to bear on these matters.[101] Their practice was infused with physical chemistry, but this was neither about reductionism, nor mechanism, nor holism and complexity in their own right. Materiality, artificiality, and models, quite simply, were integral in the daily life.

In the interwar period, the 'true secrets of this world' were not 'dug up from the dusted libraries and they aren't to be found in the dark chambers of the laboratories. One only has to open up one's eyes in order to discern them always and everywhere.' Books such as Kahn's popular *Das Leben des Menschen* (1926) thus casually outlined the mysteries of the protoplasm by walking the reader through 'everyday foams' - beer, champagne, lemonade, soap. For, the cell too was but more of the same: 'The protoplasm, a foam! Grand, proud man – a creature of foam!' 'The secret of foam', in turn, was 'spoken in one word – Surface!'[102] This was a true 'surface world' as Donnan concurred, albeit in a rather more specialist *Introduction to Surface Chemistry.* It was of the 'highest importance for the understanding of great regions of natural phenomena' generally, and of course, there were the great many phenomena of life which were 'intimately concerned with the actions occurring at surfaces'.[103]

If in the nineteenth century the *cell* had gradually been taking shape as static tissue slices on microscope slides, this now gave way to a dynamic, teeming aggregate of forces, energies and processes. Not coincidentally, the only major historical study on twentieth century cell biology emphasized the manifold intersections of this history with the history

[101] Esp. Garland E. Allen (1975); Roll-Hansen (1984); Lindner (2000); Fangerau (2009).
[102] Kahn (1926): pp.22-23.
[103] Rideal (1926): preface.

of cinema. Hannah Landecker's work has shown how this dynamic cell came into being at the precise moment pictures began to turn into moving pictures.[104] Cinematic celluloid film soon became a standard representational medium of cells - for the purposes of research, education and entertainment alike. And as I shall argue here, not only turned cells dynamic *on* film, but *as* films: 'no less than a fourth state of matter', as Sir William Hardy enthused. These 'films' had little to do with 'the cinema', Hardy explained at a 1926 evening lecture entitled *Films*, but with the 'film spread over the surface of each living cell' and 'those thin films of matter, familiar to all in the form of soap bubbles or lubricating films of oil'.[105]

Familiar to all: Films, surfaces, membranes, it was common knowledge, mattered to life - modern, industrial, and organic. Surface phenomena had turned into a world both familiar and remote, natural and artificial. Novel techniques - ultra-microscopes, micro-surgery, ultra-sonic waves, quick-freezing, ultra-centrifuges, high-speed photography and more – were actualizing the *cell* into a temporalized *entity*: a question of phase-reversals, surface tensions, elasticity, gel formations, viscosity changes. Biologists despaired over the question as to whether one still dealt at all with 'material changes' to be 'seized optically'.[106] On the horizon one could now discern a 'dynamic morphology' which, Cambridge zoologist James Gray believed, had to 'creep downstairs' to the levels of biophysics and molecular physics.[107]

Advances, evidently, weren't confined to the laboratory. The modellers of cellular life in the laboratory were surrounded by a general fascination for the collapse of the artificial and the natural that was provoked by the universality of colloidal behaviour and an omnipresent, two-dimensional world of surfaces.[108] At the Century of Progress exhibition in Chicago in 1933 'Visits to the World of Cells' had first become a reality. To the delight of educators, '[m]otion, plus light, plus pictures, plus sound ..., plus grotesqueness in

104 Landecker, Maienschein, Glitz, and Garland E. Allen (2004); Landecker (2005); Landecker (2007).
105 See 'Films' [Royal Institution of Great Britain, 1926]. #47 in Hardy (1936).
106 Spek (1925): p.900.
107 Gray (1931): p. viii.
108 Orvell (1989); J. Ward (2001); Cordeschi (2002); Botar (2004).

construction' met the challenge to convey not 'static' ideas, but the 'outstanding vital processes' of the cell.[109] 'Should we wonder that Life, being a form of colloidal behaviour', as Korzybski's *Science and Sanity* (1933) asked, 'presents a similar character on macroscopic levels?'[110] In the period between the wars, the conflation of ontological realms, between the synthetic and natural, micro and macro, the organic and artificial, the real and ersatz, itself turned mass-ware.[111] Was it not wonderful, as *The Chemistry of Familiar Things* (1924, 4th edition) asked, 'how each organism produc[ed] its kind and quota of chemical substances'? Beeswax was a 'perfect plastic substance', lac insects supplied shellac, and in 'the realm of fibers we have the spiders and silkworms' which man in his creations of 'artificial silk' was only beginning to imperfectly 'duplicate'.[112]

The likes of a Fischer and Clowes, in duplicating cellular life, participated in this discourse. But if the vision of life, and the type of model-experiments they pursued was intelligible and persuasive, it was because it occurred at a time when the 'social life of things' generally was shaped, profoundly, by substitutability.[113] The more thoughtful interventions into this realm of replaceable materials may have been concerned with the subtler analytic distinctions such as that between the 'substitute' ('the reproduction of only the external appearance') and 'surrogates' ('the reproduction of internal properties'), the general advent of artifice, however, was not about aesthetics, but economics and nationalism.[114] The Great War had triggered an unprecedented search for *substitute* products - coffee, gum, rubbers, fertilizers, fuels, explosives - a trend intensifying in the autarky-conscious interwar period.[115] Even the 'pure, good' coffee-substitutes such as succory that already had been around now had to be substituted, analysed, and improved on as was true for a great many other products, whether natural, organic, metallic, semi-synthetic or

[109] Thone (1933); Pearson (1935): p.149.
[110] Korzybski (1933): pp.121-122 .
[111] Esp. Bud (1993): chapter 3.
[112] Sadtler (1924): pp.1-3.
[113] On this notion, see Appadurai (1986).
[114] Lehner (1926): preface.
[115] Aftalion (1991): pp.181-186; Marsch (2000): pp.230-231; Heim (2003).

artificial.[116]

A whole new world of increasingly synthetic, and increasingly colourful materials - bakelite, viscose, margarine, cellophane, synthetic vitamins, rayon ('artificial silk') – swamped interwar economies[117] If not everything turned wholly synthetic, useful things such as soaps, textiles, semi-synthetics or foodstuffs now were not only complex phenomena, but well-charted ones at that. This included such uncannily life-like phenomena as the 'salting out' of soaps - ion-induced precipitation phenomena; the stability and dynamics of soap film formation; even, as James McBain wrote in 1921, 'the study of the[ir] life-history ... or formation in its genesis and subsequent transformations'.[118] James McBain, as noted, was himself one of those far-ranging students of colloidal behaviour renowned for having 'considerably broadened our knowledge' of soap phenomena.[119] Their significance, and deep resemblance, to biological problems was more than obvious. Readers of the *Journal of General Physiology* knew: most of these phenomena had been 'far more extensively studied in the case of soaps than for any other class of substance'; not least, the ones on which 'commercial soap manufacture' depended.[120]

It was, in other words, a small step to turning these mundane substances into biological ersatz. If it hadn't been palpable, the logic of the approach was made explicit in works such as *Methodology of the Imitation of Life Processes through Physical Constellations*, published in 1921 as part of the *Biologische Arbeitsmethoden* series, or Richard Beutner's widely received monograph *Die Entstehung Elektrischer Ströme in Lebenden Geweben und ihre Künstliche Nachahmung durch Synthetische Organische Substanzen* (1920), revised and republished in 1933 as *Physical Chemistry of living tissues and life processes, as studied by artificial imitation of*

116 Sayre (1918): p.112; Pritzker and Jungkunz (1921).
117 From a history of science/technology perspective, see Meikle (1995); Mossman (ed.) (1997); Westermann (2007): chapter 1; Bächi (2008); more generally, see Orvell (1989).
118 Darke, McBain, and Salmon (1921): p. 395.
119 Kruyt (1927): p.240; On McBain, see Rideal (1952).
120 McBain and Kellogg (1928): p.3.

their single phases.[121]

The *Methodology,* penned by Ludwig Rhumbler, Professor at the School of Forestry in Hannover, ranged widely through the world of artificial processes, not without warning, however, of the distance between 'the artificial products hitherto recognized ... [and] the fundamental performances which constitute Life'. A mere 'symbolic or allegoric imitation' was easily achieved, but resulted, so Rhumbler, in treacherous 'artifice' [Kunstgebilde] at best. Rhumbler's 'imitation experiments', in contrast, targeted not mere 'external resemblance' but the realization of 'physical analogies'. Here was the logic of such models: choosing the suitable ingredients, composing an artificial system, testing its physical characteristics, finally, comparison with the biological reference system.[122] By maximizing the 'number of parallels' between imitation and original, a 'suitably composed system of liquids', Rhumbler explained, could serve as 'indirect evidence' that physical processes 'performed', in identical fashion, in the protoplasmic substance.[123]

Performance mattered, and clearly, so did certain materials – materials understood, analysed, tested, ready-to-hand. Beutner, for his part, had received his original training in physical chemistry with Nernst and Haber. This background, clearly, made Beutner 'especially fitted ...for the task' of imitating certain living processes. Shortly before the war Beutner, now in America, had begun to construct artificial models – in collaboration, initially, with Jacques Loeb:[124] simple systems of apple or tomato peel amazingly reproduced certain bioelectrical phenomena, for instance, when brought into contact with electrolytic solutions. After the war, meanwhile having stranded at the Bakelite Company, Beutner pushed the agenda further. In his manifesto of 1920 imitation turned programmatic, exploiting materials in the same we already are familiar with:[125] Bioelectrical

121 Beutner (1920); Rhumbler (1921); Beutner (1933).
122 Rhumbler (1921): p.227; Spek (1925): p.545; on Rhumbler, see Spek (1939).
123 Rhumbler (1921): pp.221-222.
124 'Report by Dr Osterhout', 1930, OSTERHOUT, Box 3, Folder 'Rockefeller Trust'; and preface to Beutner (1920).
125 See Roughton (1927).

phenomena were to be imitated by way of so-called 'oil-chains', Beutner there proposed, composed of 'diverse oil mixtures' - lecithin in guaiacole, phenols, esters.[126] And such a compositional approach, if executed systematically, allowed for unprecedented degrees of control, and hence, knowledge of the factors entering. Oil-chains, and by proxy, the cell-surface, so became amenable to Beutner's elaborate quantitative analyses, which heavily drew on Haber's theory of phase boundary potentials.

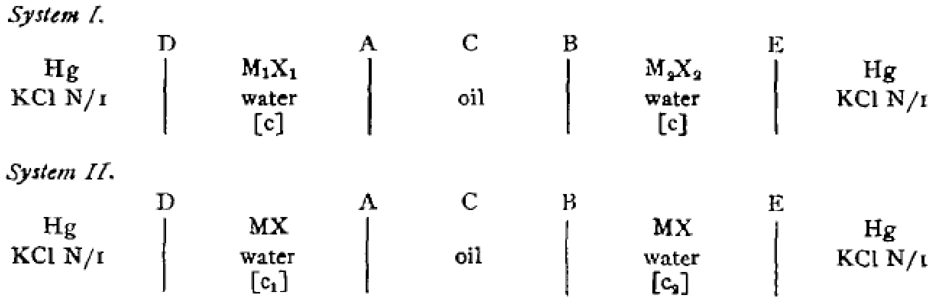

Figure 3: Beutner oil-systems

Even critical minds conceded that Beutner 'placed the study of bioelectrical phenomena upon an entirely new footing'. There were the 'most striking analogies between 'oils' and the substances which [Beutner] entitles 'physiological objects''.[127] And in manifesting such striking analogies, Beutner's oil-chains, like the mixtures of a Clowes or Fischer, functioned as what I call ersatz-objects: They mediated not only the understanding of *materials* – common and biological ones - but themselves served as stand-in objects of mimetic experimentation.

Perhaps one 'perceive[d] better than anywhere else the striking advantage of using models in the development of our knowledge of cell permeability' the renowned physiologist Rudolf Höber mused at a Memorial address at the Woods Hole Oceanographic Institute in 1929.[128] Höber, author of a highly influential work on the *Physical Chemistry of the Cell and the Tissues* (1926, 5th edition),[129] on the occasion recounted

[126] Beutner (1920); also see Beutner (1923).
[127] Haynes (1922): pp.95-98; also see nn. (1934a).
[128] Hoeber (1930): pp.16-17.
[129] See Roughton (1927).

the many ever more complex 'model experiments' that had contributed to such development; and in particular, he recounted those with 'artificial membranes' currently underway at his own institute at Kiel, artfully composed into 'layers' and 'patchwork' patterns made out of albumin, collodion, or gelatine discs. 'Intelligibility', after all, was 'the essential criterion of the scientific view.'[130] And models, to be sure, were particularly essential to the intelligibility of the cell's surface. Quite simply, because there would be nothing but ersatz; no *natural* science of the cell was discernible. Here is Rudolf Mond, one of Höber's several associates, echoing his master: 'Because the dimensions are so small, the possibility of elucidating the structure of the plasma membrane, for the time being, doesn't exist; it remains', Mond noted in 1930, 'the indirect method of investigation by way of comparison with membranes of known structure'.[131]

Though the urge to imitate found its perhaps most elaborate articulation in the (very different) works - and words - of figures such as Rhumbler, Beutners, and Höber, it is the prevalence of such practices that is of interest here; rather than, that is, anyone's exceptionalness. And it is the materiality of model-substitutions, as the next section will further explore, rather than intellectual programmes which shaped conceptions of the living. Figures such as Seifriz, Beutner or Fischer operated, no doubt, at the margins of mainstream biological science; the Höbers very close to its centre - and there were others like him, Loeb's successor as the head of the Division of General Physiology at the Rockefeller Institute, for instance, W.J.V. Osterhout, who committed himself to such models – or to what he believed was Loeb's historical mission: the 'experimental biology of the cell' and 'non-living models' thereof, as he informed his patrons in 1930.[132] But in either case, the materialities of mimetic practice mattered crucially, and over-emphasizing these or other intellectual contributions would distort what was the interwar life of the cell.

130 Höber (1930).
131 Mond (1930).
132 'Report by Dr Osterhout', 1930, OSTERHOUT, Box 3, Folder 'Rockefeller Trust'

The things themselves – *surfaces* – informed the mimetic project, and not individuals or their philosophical agendas. And as such, it wasn't tied to any particular locale; rather, it mushroomed, wherever things were studied, tested, and analysed – almost everywhere. Model-experiments were common biological practice. By 1929 a specialized text-book such as Gellhorn's *Permeability-Problem: Its physiological and pathological significance* would devote an almost excessive space to artificial models.[133] Three years later, the first volume of the *Annual Review of Biochemistry* set in with an instalment on 'Permeability'. Penned by Höber, it carried much of the same message.[134] Here, in the models one composed, it was that secure knowledge resided. Their 'heuristic value' was beyond doubt. But, the analogies so uncovered, one always had to keep in mind, might 'very well' be 'without relation to the inner mechanisms'.[135] The next section will zoom closer into these relations - and inner mechanisms.

Layers and pores

As the chemistry and physics of 'everyday life' were marching forward, the all too elusive surfaces of the cell gained palpable materiality as well.[136] Its substitute substances then almost emerged, as we have seen, naturally. But more can be said about the productivity of these material entanglements and how profoundly they shaped the permeability-problem as a problem of inner mechanisms, processes and dynamic changes. Modeling cellular life indeed was not about mere external or substantial 'resemblance'. Neither did the fabricated world of surfaces simply determine cellular nature. Here we will complicate our account: for in the details, cellular nature was as diverse, as this section shows, as this fabricated world itself. The immense and growing literature on permeability, as 'Membranforscher'

[133] Gellhorn (1929).
[134] Höber (1932); also see Höber (1936).
[135] Gellhorn (1929): p.43.
[136] Cited is Bancroft (1921): p.2.

Walter Wilbrandt surmised in 1938 in fact stood 'under the sign of the collision of two conceptions'. There were those scientists who imagined the cell surface to consist of a liquid, oily, lipoid layer, and there were those who preferred to picture this surface as a porous, sieve-like and rather solid structure. These two conceptions accounted for the penetration of substances into the cell in terms of two 'fundamentally divergent principles'.[137]

'[O]ne of my best young friends and scholars [sic]', as Höber praised him, Wilbrandt, who also had passed through Donnan's laboratory surely knew what he was talking about – hands-on.[138] From a theoretical point of view, the model-experiments discussed in the foregoing were indeed motivated, by and large, by a somewhat particularistic conception of the cell membrane as an oily, liquid layer or phase - conveniently imitated by bubbles, emulsions, foams, and soap-oil mixtures. By the 1920s, these compositional practices had become deeply associated with the so-called 'lipoid theory' of permeability and the name of one of its originators, the English-born Botanist Ernest Overton (1865-1933). A by-product initially of certain *vererbungsmechanische* experiments Overton had pursued in the early 1890s, the basic principle it stipulated was that of a 'selective solubility': very nearly, Overton found, the speed of permeation of a given substance into a cell correlated with its relative solubility in fatty oils (usually olive oil) - its 'partition coefficient'. Overton concluded that a delicate lipoid layer surrounded the cell.[139]

Some version of the lipoid theory soon was endorsed by a great many physiological scientists.[140] But nobody, to be sure, had ever *seen* a lipoid membrane; and worse, major criticisms - levelled from early on - zeroed in on the incapability of the solubility theory to deal with substances not so readily soluble in fats. Prominently among those recalcitrant

137 Wilbrandt (1938) : p.212.
138 Höber to Osterhout, 13 December 1933, OSTERHOUT, Box 2, Folder 'Hoeber'
139 Collander (1933); Overton (1901).
140 Höber (1906); Bernstein (1912): esp. p.102; F. F. Blackman (1912).

substances were electrolytes. The apparent permeation of such water-soluble substances wasn't readily explained on the assumption of a lipoid layer. Rather, it suggested that the 'surface film of the cell consist[ed] exclusively or essentially of certain proteins', as Loeb opined, for instance.[141] These and similar counter-evidences were themselves fraught with problems, however, and frequently obtained only by way of exposing cells to what presumably were 'abnormal' conditions: the conception of ions as primarily toxic, membrane-precipitating agents was widely taken for granted.

Nonetheless, these phenomena weren't easily ignored. Its perceived short-comings quickly generated several mutations of the original. In 1904, the Viennese botanist Nathanson, for instance, proposed that in order to explain the penetration of water, the surface layer should consist of a 'mosaic' of lipoid and protein elements. Others followed suit, and conceptions of the membrane as jelly-like structures, as a liquid layer of suspended lipoids and protein patches, or as an emulsion of lipoids and proteins proliferated.[142] Support, and most of all, concrete reality the lipoid theory and its diverse variations received through Modellversuche. When it came to cellular surfaces, as we have seen, one composed rather than observed. Here we will encounter other conceptions, and further models, but only so as to reinforce the point: It simply were other kinds of mundane surfaces - porous things - that generated - other - answers. Indeed, in the case of these so-called pore-theories of permeability we would find exactly the same mediation of materials, things, surfaces, membranes and models. Unlike the lipoid theory, porous easily subsumed the phenomena difficult to account for in terms of fat-solubility. But in either case, theories of the nature of the cellular surface were based, not on observations, not mere experiment and intervention, but manufacture. The complications model-makers felt prompted to introduce into their ever-more elaborate fabrications betray not so much the limitations of modeling life by inanimate means than the need to accommodate these

141 Loeb (1911): p.665; also see Ruhland (1908); Osterhout (1911).
142 Nathanson (1904); Grafe (1922); Stiles (1924).

fundamentally divergent, colliding 'conceptions'. And re-approaching cellular membranes from the perspective of porous materials thus can serve to give definition to what united such modeling-activities - quite irrespective of the kinds of mundane resources appropriated: the quest for 'inner causes'.

Perhaps for too long, as the German-born bacteriologist turned membrane scientist Leonor Michaelis alarmed in 1926, just about to move to the Rockefeller Institute, New York City, one had approached the 'membrane as a given but [one didn't] have to be concerned about the inner causes of semi-permeability.'[143] But no longer was one so oblivious. If solubility, or the mechanisms behind it, was one possible candidate for such inner causes, the fundamental principles of filtration were another. The 'analogy of the cell with an ultrafilter [was] obvious' notably Walter Ruhland had discerned still in 1913, then an employee at Biological Reichsanstalt for Agriculture and Forestry near Hannover. Based on classification of more than 100 colloidal substances according to their permeation-behaviour and particle size, Ruhland, the future professor of botany in Leipzig, had concluded that cellular permeability was 'not at all based on a solubility-phenomenon, ... but on a process of filtration, where the gels of the plasmatic membrane play the role of the ultrafilter.'[144] 'The graded series' of particles – arranged according to size - which Ruhland had determined on the basis of the latest filtration techniques thus wonderfully 'paralleled' their permeation behaviour into the cell.

Ruhland was the Clowes of pores. And this story might have begun with him: the cell surface turned into filtration technology at the moment the latter themselves turned pervasive, and their fundamental principles were exposed. The significant agent in this part of the story are filters; and more specifically, ultra-filters, particularly those made out of *collodion*, a syrupy solution of nitro-cellulose in ether, alcohol or acetate. When dried, collodion formed a thin, flexible cellulose film: stuff that pervaded the world.

[143] Michaelis (1926): p.34.
[144] Ruhland (1913): esp. p.122; also see Ruhland and C. Hoffmann (1924); nn. (1958).

In the interwar period, cellulose, ground up, nitrated and processed formed the basis of a plethora of semi-synthetic products and industries. From viscose to paints and lacquers to the more luxurious assortment of man-made materials turned into 'imitations', 'surrogates' or 'substitutes' nitrocellulose was both omnipresent and invisible, infinitely malleable in shape, colour and texture.[145] One such incarnation of nitrocellulose was collodion, whose career as a film-forming thing had been long in the making. From around 1850, collodion, thinly spread over photographic plates, was the material basis of photography (the 'wet collodion process').[146] In parallel, collodion had entered the laboratories of physiologists and chemists. Adolf Fick, in his studies *Über Diffusion*, for instance, then famously made use of the new material which could easily be moulded into thin, permeable membranes.[147] By 1900, collodion membranes were turning into standard items of the bacteriological laboratory, replacing parchment paper for the purposes of dialysis.[148] 'The raw material [being] available commercially as "gun cotton" or "pyroxylin", the 'comparative ease' of the procedure preparing them was explained, routinely, in laboratory manuals.[149]

Membranes – despite their prominence in the theoretical tool-box of physical chemistry – weren't, as Michaelis had observed, 'fictive instruments' only.[150] Far from it. Collodion filtration membranes belonged to the central, defining tools of the new colloid science, accompanying such instruments as the ultra-microscope in the quest to carve out the neglected dimensions of matter.[151] Like electro-chemical and colloidal surfaces, filtration was turning into both, a science and an industry. In 1923, the allegedly first *Text Book of Filtration* informed that filtration

> plays a primary role in all the activities of life, from the phenomenon of plant

[145] E.g. C.F. Cross, Bevan, and Beadle (1918); Lehner (1926); Bonnwitt (1933).
[146] Brothers (1899): pp.86-87.
[147] Fick (1855).
[148] Eggerth (1921): p.203.
[149] E.g. Hatschek (1920): pp.21-23; H.N. Holmes (1922).
[150] Michaelis (1926): p.34.
[151] Ede (2007): esp. pp.64-65.

osmosis to the ordinary straining of breakfast coffee. It occurs constantly on every side, although it is seldom noticed or appreciated as such.[152]

The express purpose of the book thus was to correct this ignorance, and also, to lay down 'the general laws of filtration'.[153] Similar attempts soon issued from elsewhere. The London inventor Pickard of *Metafilters Ltd.* too felt the need to survey the subject's 'scope and importance in modern life' in his *Filtration and Filters*, also tackling the 'fundamental principles underlying all filtration'.[154] No doubt, as Alban Mühlhaus of the State Research and Experimental Station for Grain Processing and Fodder Refinement, Berlin, pointed it out in 1926, one lived in a period of great advances regarding the study of 'the processes of sighting, sieving and filtering'.[155]

Like the materials dialysed, classified and purified, the materials and processes of filtration themselves turned into more transparent things. The 'ultrafilter' theory of the cell is but one example of this movement. In 1907, only a year before Ruhland first came to the fore with his investigations, the German chemist Heinrich Bechold thus had presented to the world what was a major departure as regards filtration technology: collodion filters of *graded* and *known* sub-microscopic pore-size. The industrious Bechhold, author of *Die Kolloide in Biologie und Medizin* (1912, 1st ed), most successfully disseminated his invention: 'ultrafilters', one English physiologist surmised by 1915, had 'passed into general use'. By the late 1920s, ultrafilters could be easily obtained in many a variation from Bechold's own *Membranfiltergesellschaft* in Göttingen.[156] Or one simply relied on the many advanced recipes for preparing them. Such membranes were prepared, preferably, from 'cellulose acetate varnishes of commerce' which were 'sufficiently specified' or especial 'membranogenes' such as *Kollodion Schering-Kahlbaum for the preparation of membranes*.[157]

Less overtly, the general advances in nitrocellulose-based materials pointed into the

152 See Introduction to Bryden and Dickey (1923).
153 Ibid.
154 Preface to Pickard (1929); also see Prausnitz (1933).
155 Mühlhaus (1926).
156 Walpole (1915); also see Prausnitz (1930): p.168; Bechhold, Schlesinger, and Silbereisen (1931): p.174.
157 J. Taylor (1926): p.401; Bjerrum and Manegold (1927); Keenan (1929): p.378.

same directions. Nitrocellulose-based materials were now handled easier, they were purer, more robust, and came with specific, controllable properties. Characteristic interwar developments included 'endless' foils: *cellophane*, *sidac*, *heliozell*, *cellglass* or *transparit*; cellophane, for example, in sizes 'down to molecular sieves' had the distinct advantage of not reacting with dialysed substances, one read in the *Journal of General Physiology*.[158] Such details were crucial as collodion films could be chemically 'highly reactive', in which case the mimetic evidence against 'solubility' theories they provided would be severely undermined.[159]

The immense activities in quantitative data production advanced filtration-media enabled, for their part, slowly eroded the earlier confidence in lipoid theories. Indeed, as the pores of fabricated membranes began to approach molecular dimensions, membrane-filters had long begun to live a curious double-life in the laboratories. As dimensions - both of the pores and the particles supposedly moving through them – diminished, devices of analysis turned into objects of analysis, and in a second step, into ersatz-objects of biological experimentation.

Knowing membranes, here as there, meant *making* them. And in the process, 'permeability' metamorphosed from vague concept into concrete process. Elaborate 'plan[s]' to characterise such membranes – by means of variables 'readily controlled and expressed numerically' – thus spread widely.[160] For too long had the 'routines' of 'grading membranes' been treated as 'a matter of skill which was not always definable'. The moment of subjectivity that had entered into the making of membranes was becoming unacceptable. Notably William Brown of the Imperial College, London, had announced 'a new departure' still in 1915, a routine which was 'merely mechanical'. Brown, occupied with the analysis of fungal extracts, subjected membranes to a rigid treatment of alcohol

[158] McBain and Kistler (1928); McBain and Kistler (1930); Halama (1932).
[159] Beutner, Caplan, and Loehr (1933): p.393.
[160] Walpole (1915); W. Brown (1915); Farmer (1917); Eggerth (1921); Looney (1922).

solutions of varying strengths (by 1% steps). In terms of pore size, each membrane in the resulting series was uniquely characterised by its ‘alcohol index’: the ‘strength of alcohol required for producing a membrane which just prevents diffusion of [a given] substance’.[161]

Water	—	Safranine	75–77·5
$NaCl$, NH_4Cl		Dextrin	85–87·5
$KMnO_4$	30–40	Starch	90
Picric acid	35–40	Aniline blue	92
Potassium oxalate ...	60–70	Litmus (neut.)	93
Bismarck brown ...	65 (−)	Congo red	96
Methylene blue ...	70 (−)	Night blue	>96
Neutral red	72·5–75		

Figure 4: Brown's substance-table, 1915

In due course, ‘Brown’s method’, and the practices of serial classification it enabled, entered the standard repertoires of students of permeability.[162] The diffusion of ultrafiltration was accompanied by series and tabulations of the ‘molecular volumes’ of the most diverse assortment of substances. Increasingly so, students of cellular permeability were able to avail themselves, or had at their disposal, very sharply defined means of modelisation. The precision derived from the ability to manipulate and control membrane characteristics, pore-size and composition – precisely: from ‘coarse’ to maximally ‘dense’. [163] The cell, meanwhile, was inscribed into an ever more nuanced space that was essential that: spatial, geometric - pores, filters, interstices. It meant operating within a framework that differed significantly from the one prioritizing oil-solubility as the central characteristic.

[161] W. Brown (1915): esp. p.598.
[162] Gellhorn (1929): p.24; Gicklhorn (1931): esp. pp.580-583.
[163] Collander (1927): pp.215-218 .

Tabelle I

Substanz	Formel	Mol.-Gew.	MR_D	σ
Tributyrin	$C_{15}H_{26}O_6$	302,2	76,4	—
Triacetin	$C_9H_{14}O_6$	218,1	48,7	0,758
Trimethylcitrat	$C_9H_{14}O_7$	234,1	50,3	0,871
Antipyrin	$C_{11}H_{12}ON_2$	188,2	56,1	0,912
Fructose	$C_6H_{12}O_6$	180,1	37,5	1,000
Glucose	$C_6H_{12}O_6$	180,1	37,5	1,000
Saccharose	$C_{12}H_{22}O_{11}$	342,2	70,4	1,001

Figure 5: substance-table, 1926

A central role in these developments was played by the so-called 'Finnish School'. Lead by Runar Collander, this Helsingfors-based enterprise centred on extensive investigations of 'artificial membranes'. In the early 1920s, Collander had received a Rockefeller stipend to study at Höber's Kiel Institute, and through his extensive 'experiences' with artificial membranes, Collander reported by 1927, the subject of 'protoplasmic permeability appear[ed] in a new light.'[164] Collander initially had studied copper-ferrocyanide precipitation membranes, but eventually turned to gelatine and collodion membranes (prepared according to Brown's method). For Collander, composition and control were the over-riding concerns: hitherto, the 'chemical make-up' of the membranes studied, he deplored, at best had been a 'peripheral concern'.[165]

Not any more. In a move soon paralleled elsewhere, one now artfully constructed membranes, 'charged' ones, and neutral ones, of known make-up and composed of layers and patches of collodion, albumin, gelatine, casein dyes and more. And the results obtained with such superior membranes further undermined the conception, in Collander's words, that the 'permeation capacity' of lipoid-soluble substances was invariably greater than for lipoid-non-soluble substances. Particle-size not solubility, in other words, was a crucial factor determining permeation.[166]

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164 Collander (1926); Collander (1927): p.213; also see Collander (1932): on Collander, see Gerard, 'Visit to Helsingfors', 12/13 December 1934, RF/RG.1.1, 700 Europe, Box 18, Folder 131.
165 Collander (1927): p.213; p.221.
166 Mond and F. Hoffmann (1928); Höber (1930); Gicklhorn (1931); Collander (1933).

The analogical behaviour of manufactured membranes, however, like those of oily layers and phases, only went so far: permeation through porous membranes composed purely of proteins, gelatine diaphragms, for instance, even differed profoundly from the behaviour that was observed in (certain) real cells. Membrane-actions, not too surprisingly, crucially depended on the choice of ingredients. And as students of permeability came to realize, lipoids still had to be assumed as determining physiological permeability, even if indeed, the smaller a molecule, the further its permeation behaviour deviated from its lipoid-solubility. Relative to penetrating substances, Collander wrote on the occasion of Overton's death in 1933, one now had to 'ascribe to living protoplasts a certain ultrafilter action'; as far as 'Overton's hypotheses' were concerned, however, 'the last word ha[d]n't been spoken'.[167]

Colliding conceptions: Synthetic efforts such as Collander's (aptly called the 'lipoidfilter' theory) were geared towards unifying these opposing principles, 'experiences' and data. But the rapid progress regarding 'molecular surface structures' of recent, or so one reflected at the time, clearly had had the effect that 'conceptions' about membranes, now were 'less oriented towards systems of the macroscopic world'.[168] Around 1930, the utopia of precise knowledge-through-making was threatened by other, new forms of uncertainty. Given the 'dimensions under consideration', or this was the consensus that began to form among students of membrane, it wasn't clear any longer what it meant to talk of 'solubility' or 'porosity'. In all likelihood the principle was about neither, or both; such concepts, at any rate, unlikely applied at all on these scales. [169] Talk of *things* such as 'sieves', 'filters' or 'emulsions', that was, had become suspect. Here one entered unfamiliar territory, far far removed from the macroscopic world. Or so it seems, the remainders of this chapter argue, on first glance.

[167] Collander (1933): p.231.
[168] Wilbrandt (1938): p.212.
[169] Höber (1930): p.3; Collander (1932); Danielli and Davson (1935): p.496.

Molecular conditions at the surface

In the course of the interwar period, models of the cell, there is no question, gradually began to lose what once might have been their intuitive, palpable and material persuasiveness. Not even apparently simple model-systems were transparent without a considerable amount of formal, abstract and elaborate analysis. Worse, the familiarity of concepts began to dissolve in the micro-dimensions of the molecular structures. Still, the familiar things, ersatz, and the materialities of models persisted. Less explicit, as we shall see, and less ostensibly mimetic, but, and this is the point, no less significant. Molecules had to be imagined; surfaces were palpable.

Overemphasising the molecular in our stories removes from view other, and less obviously relevant sites of knowledge production. And, as the following suggests, it means to underestimate the complexities and ambiguities of the 'molecular' itself, and its manifold entanglements with the less esoteric and abstract dimensions of both, living and non-living matter. To conclude this chapter, let us turn to what is indeed very easily overlooked: the material, macroscopic mediations of what emerged at the time as one such synthetic conception of the membrane, something neither straightforwardly about pores nor solubility: the iconic bi-layer (or pauci-molecular) model of the membrane. This molecular *representation* of the membrane, I shall argue, is best read as a case of modeling as substitution: surfacing in 1935, the model crucially depended on the materialities of *ersatz*.

The study and 'artificial production of monolayer films' in fact was just about to begin to yield crucial insights into many vital processes, or so the *Times* reported of the 'Mysteries of Surface Action' in 1937; the reader was invited to 'reflect that every cell possesses several surfaces'.[170] An expression of the unabated excitement, three special

[170] nn. (1937b): p.7.

meetings brought together membranes, models and artificiality in Britain during 1936/1937 alone: two symposia on surface phenomena in biology, and one on *The Properties and Functions of Membranes, Natural and Artificial*.[171] Studies with artificial membranes might seem as 'heroic or ... naive' as the flute-playing automata of the eighteenth century, as Höber had ventured the year earlier, meanwhile at the University of Pennsylvania. But they certainly allowed for deep insights into the 'nature of life'.[172]

Indeed. Rewind a few years - fall 1934: 'Even if the plasma membrane were an emulsion membrane it still would not do so. [Clowes'] theory is much too crude'. So read a letter to the model-maker Osterhout, penned by James Danielli. As a recent product of Donnan's two-dimensional surface world, Danielli had begun to ponder quite different things at the time: the 'meta-stability' of unimolecular films, dynamic equilibria, and 'micelles', he gasped, 'constantly breaking down and being reformed'.[173] He was busy 'endeavouring to find some reason, theoretical or experimental, for completely eliminating the possibility' of an emulsion membrane.[174]

Only months later, Danielli burst on the scene, together with his friend and UCL colleague Hugh Davson, advancing a new 'model for the cell surface'. Pictured on paper, it still looks familiar:

[171] nn. (1937a); nn. (1937b); nn. (1937c).
[172] Höber (1936): p.196.
[173] Danielli to Osterhout, 28 November 1934; Danielli to Osterhout, undated (1935), OSTERHOUT, Box 1, Folder 'Danielli'
[174] Ibid.

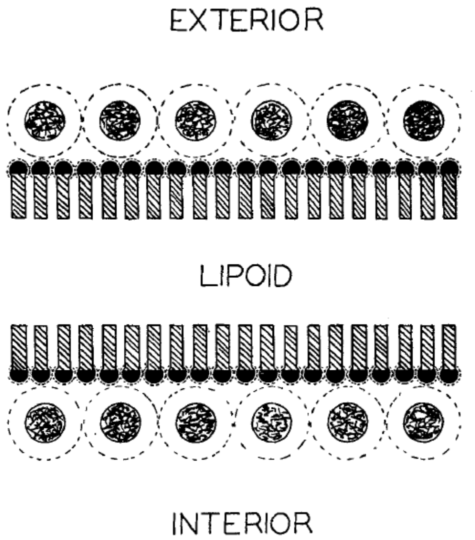

Fig. 1 **Schema of molecular conditions at the cell surface.**

Figure 6: the paucimolecular model, 1935

Depicted were the 'molecular conditions' at the cell surface. Given these remote dimensions, this surface was to be conceived, Danielli and Davson declared, not as a liquid solvent, nor, as one might alternatively have supposed, as a 'rigid pore structure'.[175] Rather, it had to be imagined as a 'very thin lipoid film with a protein film adsorbed upon it'.[176]

Not surprisingly so: such thin 'monofilms' were a subject, as IG-Farben's Hermann Mark observed in 1933, 'at home particularly in England'.[177] Within England, it was at home, not least, at University College London. Danielli and Davson had graduated from there in 1931, at a time when the chemistry department flourished under its head, impresario of colloid science Donnan. Davson subsequently transferred over to biochemistry, and by 1934 found himself studying the aetiology of glaucoma on the behalf of the MRC Industrial Health Research Board (and Donnan equilibria in the vitreous body of the eye in particular).[178] The following will focus largely on Danielli (nothing will be lost in doing so), who himself had graduated with a thesis on the structure of steroids supervised by Neil Adam. Adam, for his part, was the leading British authority on

[175] Danielli and Davson (1935): p.496; on Danielli, see Stein (1986); on Davson, Tansey (2004).
[176] Danielli and Davson (1935): p.498.
[177] Mark (1933): p.199.
[178] Duke-Elder and Davson (1935); Lyle, S. Miller, and Ashton (1980).

'monofilms'.

A Cambridge man, Adam himself had only recently arrived in London on an Imperial Chemical Industries fellowship. Much of the 1920s, Adam had spent in provincial Sheffield, and he was just about to publish his manifesto when moving to London, *The Physics and Chemistry of Surfaces* (1930). Widely influential, it discussed surface phenomena, as Adam put it, rigorously from 'the standpoint of molecular theory'.[179] At UCL, one accordingly found oneself at the epicentre of thin films as seen from the nascent molecular standpoint, a vision of exactness that had been cultivated and fostered, if from very different vantage points, by both Donnan and Hardy.

Much of the surface-enthusiasm in Britain, as seen, was home-made - and entangled with products. While Donnan had continued expanding his UCL empire along such directions, Hardy had made a reputation for his untiring efforts in matters of cold storage, transport, perishable food stuffs and hence, the Empire. Refrigeration had turned into an 'essential part of everyday life'; Hardy had emerged as the director of the D.S.I.R. Food Investigation Board (FIB) and head of the Low Temperature Research Station for Biophysics and Biochemistry, Cambridge.[180]

It was notably from here that Hardy exerted his diffuse influence on Britain's world of surface science. The Cambridge Station would be a 'central laboratory', on Hardy's scheme of things, where investigations into animal and vegetable 'products' could be pursued with 'exactness'.[181] '[M]uch fundamental scientific work can be done upon the behaviour of living matter and dead tissue at low temperature', Hardy had opined in 1919, when plans for the Station got rolling.[182] From here issued significant investigations into the alterations protoplasmic structures in fruit, vegetables, meat, muscle, eggs underwent upon freezing. And from here issued such works as *Permeability* (1924) which would remain

179 Adam (1930): preface; Ostwald (1931): p.103; on Adam, see Carrington, Hills, and K.R. Webb (1974).
180 nn. (1934d): p.605; also see, Roberts (1997).
181 Hardy to Shipley, 15 September 1919, DSIR 36/3800; also see Callow (1948); Hutchinson (1972).
182 Hardy, 'Proposed Erection of A Cold Storage Station at Cambridge' (November 1919), DSIR 36/3800

for many years to come the single comprehensive survey on the subject available.

Permeability was penned by the botanist Walter Stiles, otherwise known for his *The preservation of food by freezing with special reference to fish and meat: a study in general physiology* (1922).[183] And moving in the circles that formed around Hardy were the likes of R.A. Peters, Francis Roughton, Joseph Needham, as well as, notably, Adam and the already mentioned Rideal. To them especially were due some of the subtler advances in surface science at the time. In the early 1920s, Adam thus significantly advanced the analytic methods in use for the study of thin films. We will hear more on these so-called surface-tension techniques shortly. Rideal, meanwhile, pursued surfaces along mostly electro-chemical lines and in 1930 was launched - thanks to Hardy's efforts - on a newly created chair for Colloid Science at Cambridge.[184]

There, all manner of surface materials were tested, analysed and fabricated in the hope of elucidating their structure and behaviour: films formed by snake venoms, composite films of oxygen and hydrogen on tungsten, myosin films, benzalazine vapour formations, monolayers of proteolytic enzymes. By 1935, Rideal successfully had injected advanced courses on 'Biocolloids' into part II of the Cambridge Tripos.[185] Once in London, Adam too had turned to films of a more complex character, largely in collaboration with ongoing efforts at the National Institute of Medical Research. The 'peculiar knowledge' of surface chemistry, as its director, Henry Dale, opined, had to be brought into 'closer, and indeed, obligatory relation with medical problems'.[186]

And this relation was to be directed, notably, at the characterisation of sterols; particularly, of vitamin D, a substance which spawned considerable commercial excitement. The whole science of vitamin D, as one Rockefeller Officer recorded on a visit to London

183 Stiles and Adair (1921); Stiles (1921); also see Hardy (1926); Moran (1930); on Stiles, see James (1967); also see Laties (1995).

184 Report on the Council of the Senate on the Rockefeller Foundation, 27 April 1931, CUL/ULIB 9/4/4; and see Kohler (1991): pp.185-187.

185 Report on Committee on Biocolloids, Minutes 4 June 1934, CUL/University/MIN.V.68

186 Dale to Mellanby, 7 September 1933, FD 1/3451

(somewhat appalled), was especially 'mixed up with industry' and 'tainted'.[187] Unfortunately, as *Vitamins: A Survey of Present Knowledge* (1932) deplored, vitamin D was unstable and 'aged', losing its 'antirachitic potency' within hours and days.[188] However, such potency could be unleashed by UV-irradiation, investigators at the NIMR having identified ergosterol as vitamin D's stable, photosensitive 'parent substance' in 1927. Adam subsequently became involved with investigations into ergosterol's 'irradiation products'. And with Danielli's assistance, he took up systematic studies of ergosterol-films and their (in)stability.[189] They were formative as to Danielli's eventual ideas on cell membranes.

The vitamin investigations themselves were a routine application of a matured research technique: 'comparatively easy and rapid to carry out'.[190] And as a technique for the study of molecular structure, the basic principle was simple. Surface film techniques exploited the pressure that films developed when spreading out on a liquid. Essentially, this involved measuring the force an expanding film exerted against a barrier floated in a liquid-filled trough. And it yielded two types of information: area and 'surface pressure'. Film formation, significantly, was an essentially dynamic and temporal phenomenon, an aspect captured by plotting area against force:

[187] Gerard, 'London: October 8- November 17' (1934), RF/RG.1.1. Projects, 700 A, Europe, Box 18, Folder 131, p.21; more generally, see Vernon (2007); Bud (2008).
[188] HMSO (1932): p.81 .
[189] Ibid., pp.185-187 and Donnan to the MRC, 17 June 1935; Adam to Mellanby, 14 June 1935, FD 1/3451.
[190] Adam, Askew, and J. F. Danielli (1935): p.1787.

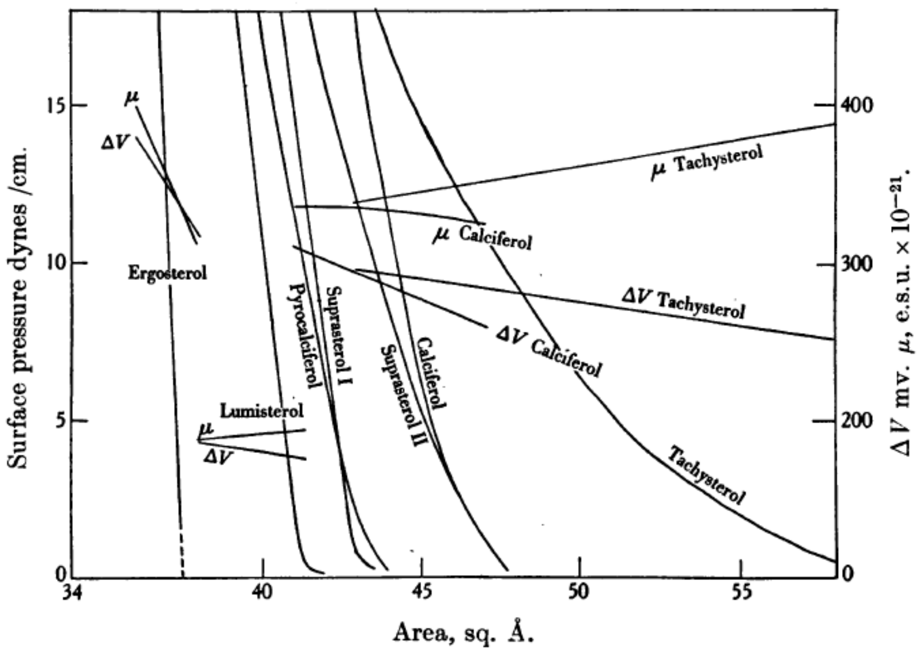

Figure 7: ergostol and irradiation products (surface pressure vs. area), 1934

But to arrive at structures, diagrams had to be 'interpreted'. It were only the surfaces and films that were palpable, not the molecules. Fairly easy, Adam explained it, was 'to infer ... the state of cohesion of the films from the course and the shape of the curves'.[191] Small area and low surface pressure, for instance, was a sure sign of high cohesion.[192] But generally, the films so studied were relatively unstable, due to oxidation, evaporation, and temperature-changes, all of which meant complex interpretational challenges. And ergosterol clearly belonged to the more complex type of film. Indeed, here one had encountered a 'curious feature' - 'abrupt' and 'considerable changes in tilt of the molecules ... as irradiation proceeds.'[193] Molecules, it transpired in these investigations, had to have 'very peculiar properties' in order to form 'stable' films.[194]

It was notably Danielli who would transfer this filmic expertise onto another object, the cell surface. There was not mere transfer, significantly: details will return us to macroscopic, fabricated things *mediating* the substitute nature of the cell far beyond overt

[191] Adam (1931): p.126.
[192] Danielli and Adam (1934): pp.1584-1585.
[193] Ibid., pp.1586-1588; p.1591.
[194] Adam (1931): pp. 129-130; p.138.

transference. Given the opacity of the surface-technique, thin films themselves evidently oscillated, quite generally, and uneasily, between tool and object. Its ambiguous character was something appreciated well enough. Given the 'immense importance to biology of surfaces', as Adam praised the technique, writing to his MRC patrons, the 'good deal' of knowledge it so far had generated about the 'simplest kinds of membranes' should provide a basis to tackle these more complex films as well.[195]

The pedagogy of surface films, on the other hand, had impressed on Danielli not only the imagery of molecules. Equally at issue were palpable phenomena of surface dynamics, structural change and stability. The 'question of stability of thin films is a very complex one', Danielli wrote in letters penned at the time. The 'vast majority of apparently stable films are actually in metastable, and not true, equilibrium.' 'The whole', it had to be imagined, '[was] in dynamic equilibrium'.[196] A complex whole that wasn't readily intuited. And not least therefore, as we shall see now, not only the molecular structure of such very unstable films as vitamin D mediated the fundamental structure of the cell surface. It did, but when it came to the life of films, this was not only a world of molecules, but as such, a loosely connected world of surfaces, organic and non-organic, of products, of mundane substances and materials. There were oils, meat, lubricants, fish and frozen gelatine, fruit stored and transported, and films forming on metal surfaces. And there were such membrane-forming things as soaps and emulsions.

More bubbles

Follow the materials: The model's immediate lineage takes us to Princeton, where Danielli had spent the years 1933-1935 to work with Edmund Newton Harvey. Director of the Physiological Laboratory, Harvey just recently had launched a journal, the *Journal of Cellular*

[195] Adam to Mellanby, 14 June 1935, FD 1/3451

[196] Danielli to Osterhout, 28 November 1934; Danielli to Osterhout, undated (1935), OSTERHOUT, Box 1, Folder 'Danielli'

and Comparative Physiology, and like Danielli, Harvey had a penchant for surfaces. In Princeton, as one biophysicist wryly observed in the spring of 1935, one was 'discussing, as usual, merely the surface of the cell': 'Harvey described his experiments with latex rubber balloons; and a chemist from Donnan's laboratory ... told the poor biologists all about surfaces, in the properly ex-cathedra tones used only by the prophets from Sinai.[197]

Little wonder. Danielli never had to sit through tedious classes on histology, or patiently train his eyes as a student on the morphological detail preserved in histological slides. This was not the cell Danielli knew. Danielli's expertise concerned the dynamic behaviours of thin films. And there was not much else to tell at the time about the *physiology* of cells but surfaces, as we have seen, because of, rather than despite, the many vivid representations of the cell that had been circulating. More important to Danielli's modelisations, however, than latex rubber balloons would be another one of Harvey's dynamic creations of surface-phenomena. Indeed, it was a true filmic experience of cellular films which Harvey had realized in collaboration with Alfred Loomis, New York banker, millionaire and latter-day amateur scientist. Dating back to Loomis' involvement with 'supersonics' (and submarine detection) during WWI, Loomis himself had a long-standing interest in biophysical phenomena, and the effects of ultrasonic vibrations on biological materials in particular.[198] At Loomis' private research laboratories at Tuxedo Park, the two of them turned such 'high intensity sound waves' to great 'biological effect': 'whirling of the protoplasm', its 'disintegration (emulsification?)' and other 'expression[s] in cells of more general physical and chemical phenomena in liquid media', as Harvey announced in 1930.[199] Meanwhile, the 'analysis of the destruction' so induced had required developing a system of 'high speed instantaneous photograph[y]'.[200]

197 Hecht to Crozier, 26 March 1935, HECHT, Folder William Crozier, File 1932-1934
198 Alvarez (1980): pp. 316-319.
199 E. N. Harvey (1930): pp. 306-307.
200 E. N. Harvey and Loomis (1932).

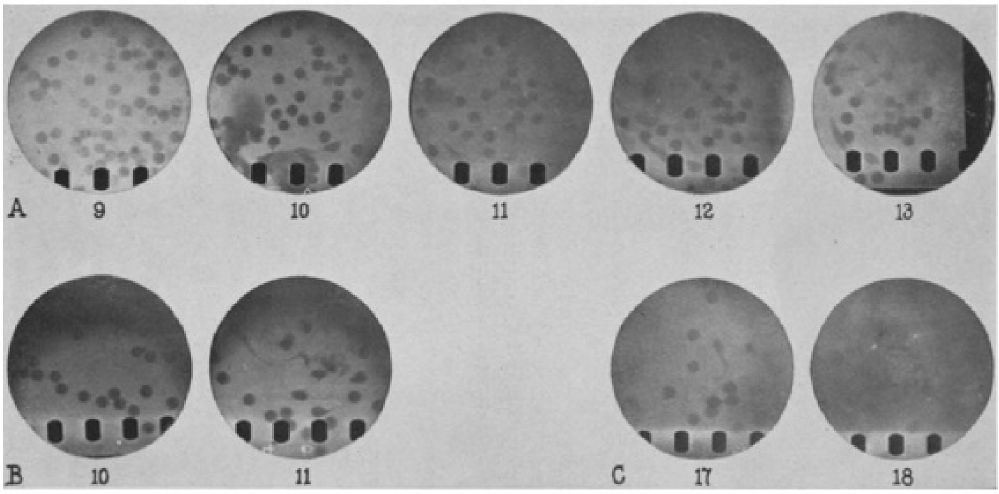

FIG. 3. Photographs of unfertilized eggs of the sea urchin, *Arbacia*, subjected to high frequency sound waves, each picture taken 1/1200 second apart. Exposure about one millionth second. The numbers give the picture sequence. The sound waves were started at the sixth picture. A, B, and C are different series of pictures.

Figure 8: sea urchin eggs subjected to 'supersonics', 1932

This system produced 'moving images' of disintegrating cells at 1200 pictures per second, and a similarly dynamic effect was achieved by a similar inventions of theirs, the so-called microscope-centrifuge: with it, 'living cells [could] be observed while ... being centrifuged'.[201] The set-up exploited a similar principle of high-frequency intermittent illumination, they reported, so that 'the appearance [of the cells] will be that of a succession of images, a moving picture.'[202]

It was a dramatic cellular spectacle. But it was not meant for the entertainment-seeking eyes and slow grasp of the layman. Significantly they had, as Danielli perceptively observed, 'at least a superficial similarity' with the formation and disintegration of soap bubbles.[203] And this was no trivial similarity. Prompted by something of an anomaly that Harvey had hit upon in the course of 'test[ing] the possibilities' of the device, Harvey teamed up with Danielli to investigate 'the physical basis' of these phenomena.[204]

In his initial explorations, Harvey had turned to very 'simple' cell-like objects such as the very nearly spherical sea urchin eggs. Conveniently, such simplicity allowed to

201 Ibid., pp.147-148.
202 E. N. Harvey and Loomis (1930); E. N. Harvey (1931a): p.268.
203 Danielli (1936): p. 399.
204 E. N. Harvey (1931b): p.269; J. F. Danielli and E.N. Harvey (1934): p.483.

consider the cell-as-egg as a 'droplet' and infer its surface tension from 'the centrifugal force necessary to pull the egg apart'.[205] These deformation studies revealed surface tension values surprisingly low - much lower than anything previously estimated. Notably the eggs of the mackerel were a real treasure grove as far as the visualization of interfacial phenomena was concerned: they contained an oil globule visibly 'flattened' against the egg's outer membrane when centrifuged. But, 'the question arises', so Harvey in 1934, 'as to the meaning of this low tension'.[206]

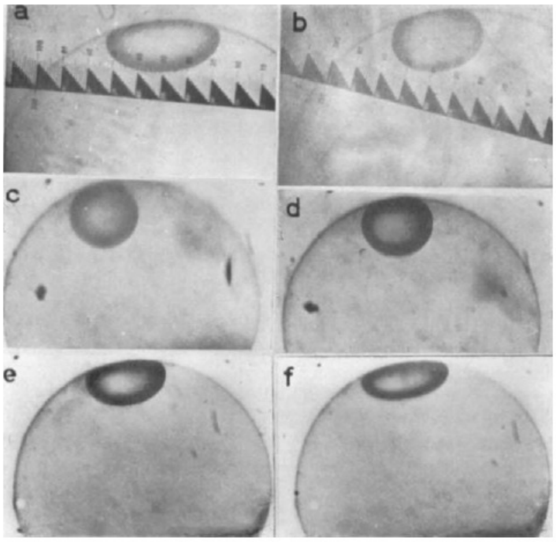

Fig. 1 a, oil globule of a fertilized mackerel egg, centrifuged at 97 times gravity. T = 0.54 dyne. b, oil of an unfertilized mackerel egg. One hundred and eighty-five times gravity. T = 1.18 dyne. c, d, e and f, single whiting egg centrifuged at 7, 62, 195 and 400 times gravity, to show progressive flattening of oil drop.

Figure 9: flattening oil globules, 1934

Mackerel eggs, oil globules, whirling of protoplasm, high-speed photography. Here then, one encountered - most palpably - basic questions of film-stability. And with Danielli's input, it was quickly determined that the low surface tension likely was caused by an previously unrecognised, protein-like substance in the aqueous part of the egg. Moreover, in order to reduce the surface tension in the manner observed, 'a film of [this] protein-like material' would have to be adsorbed on the surface of the oil phase, both films being 'approximately unimolecular'.[207] This would yield a stable film. And, it yielded half the bi-

205 E. N. Harvey (1931b): pp. 273-276.
206 E. N. Harvey and Shapiro (1934): p.262.
207 J. F. Danielli and E.N. Harvey (1934): pp.490-491.

molecular ‘schema’:

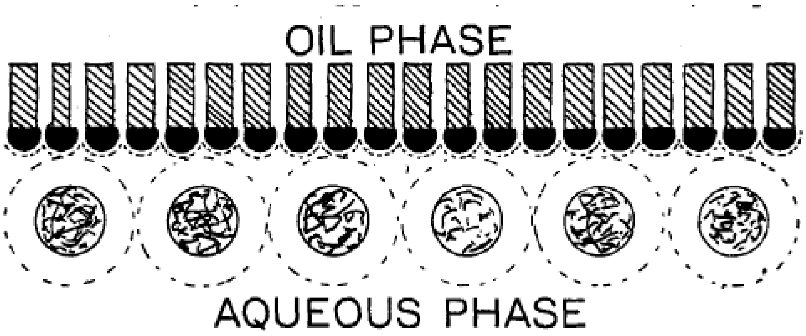

Fig. 5 Schema of molecular conditions at interface, oil—aqueous egg contents. Hydrated protein molecules on bottom, oil molecules on top.

Figure 10: proposed 'schema', 1934

The idea of the cellular surface being composed, somehow, of both lipoids and proteins, as we know, was hardly original; even the idea of a bi-layer arrangement - of lipoids - had been proposed before.[208] Danielli, however, brought his special expertise to the subject. Disturbed by the ‘particular vagueness’ with membrane structures had hitherto been ‘defined’, Danielli now set out to arrive at an ‘accurate dynamic picture’. And accurateness was mediated not by molecular representations but by the materiality of things: In order to reduce the vagueness of definition, Danielli had turned to certain ‘known properties of models’.[209]

This dynamic, accurate picture - the double-layer model - indeed returns us, somewhat unexpectedly, to the outset of this chapter, the mixtures and emulsions and thus, the familiar, macroscopic world of materials. The question concerning the ‘basic structure of the plasma membrane’, as Danielli explained it, was best resolved by way of obtaining, ‘experimentally’, ‘some spherical shell films’: soap bubbles. Underneath the visually depicted ‘molecular conditions’ printed on the pages of Harvey’s *Journal* lurked a less abstract world of materials and practice. There lurked, for one, Danielli’s investigations into the ‘mode’ of bubble formation of such spherical films: dripping salt solution into a liquid lipoid revealed that films of pure lipoid were ‘extremely fragile’. If, however, ‘a little

[208] See esp. Gorter and Grendel (1926a): p.439; Gorter and Grendel (1926b).
[209] Danielli (1936): pp.393-394; p.397.

protein' was added, this substitute-system yielded films 'much more stable and easy to handle' as was clearly ('diagrammatically') visible in formation series such as the following:[210]

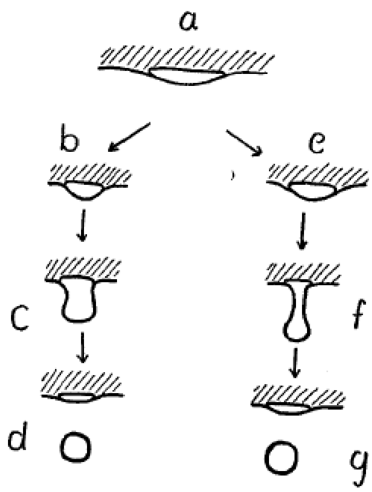

Figure 11: bubble formations, 1935/36 (left: high surface tension; right: low surface tension)

This line of approach was promptly expanded, squarely inscribing the bi-layer model, despite its molecular sophistication, into the horizons of contemporary mimetic experimentation. Experiments on the elasticity of bubbles of soap, lecithin, egg white, and various mixtures of these substances confirmed the crucial importance of the adsorbed protein layer: Only films containing protein had the 'very marked elastic properties' characteristic of cellular surfaces. And only those films resembled the disintegrative behaviour as witnessed in the ultracentrifuge-microscope.[211]

All this model-behaviour left 'little doubt' as to the type of the molecular structure of the cell membrane. It was, concluded Danielli, structurally similar to certain films that 'occur[ed] in soap bubbles and [were] known as the 'first order black''. These were not only extremely stable; what was more, in this case the presence of a double layer of adsorbed protein molecules was 'quite certain'. [212]

210 Ibid., p.393.
211 E.N. Harvey and Danielli (1936).
212 Danielli (1936): pp.395-396.

Not coincidentally, of course, and it was via soaps that the bi-layer model incorporated the mundane, synthetic knowledge most intimately. Soap films, as we have seen, was a well-charted, material world of complex phenomena.[213] Figures such as colloid scientist McBain, ever-aware of the wider ramifications of their researches, had come to defend elaborate, dynamic views of soaps where film-stability was due not only to monolayers but also 'ionic micelles or larger aggregates of molecules play[ed] some part'.[214] By the time Danielli turned to cellular surfaces, a more economical vision of soaps had begun to gain ground. This vision went back, in fact, to investigations of Lord Rayleigh. But it was 'only recently that accurate information has accumulated' to make the vision concrete as one member of the new avant-garde of soaps-scientists, A.S.C. Lawrence, surmised: 'To explain the existence of the soap film', his *Soap Films: a Study of Molecular Individuality* (1929) informed, 'it has been suggested that it has a sandwich structure'.[215]

'The real problem of the soap film [was] that it exists at all.' Having worked his ways upwards to the prestigious Royal Institution from humble beginnings – a B.Sc. from the Polytechnics of Wandsworth and Battersea and as a laboratory assistant to John T. Hewitt (an 'expert on wine and spirits' among other things) - Lawrence belonged to those pushing the study of soaps to a new level, the 'eccentric' 'individuality of soap molecules'.[216] Lawrence had become particularly concerned with problem of soap 'thinning' and its limiting extreme. This extreme we have already encountered: the so-called black film.

213 On the historical background, see esp. Schaffer (2004).
214 Adam (1930): p.138; Rideal (1952): p.543.
215 Lawrence (1930): p. 263.
216 Lawrence (1929): pp.131-132; E.E. Turner (1955): p.4493; nn. (1971): p.8.

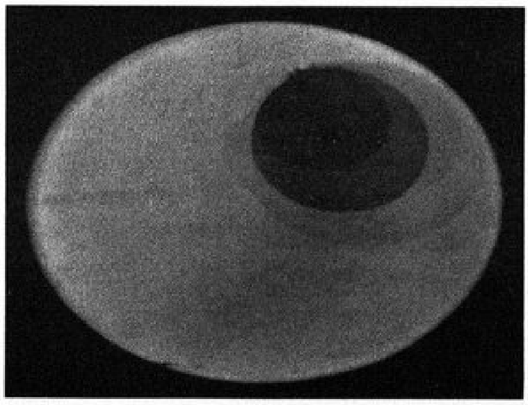

FIG. 38.—First and second orders of black surrounded by greys in stratified film.

Figure 12: Black film, 1929

'[T]he black', Lawrence was confident, almost certainly consisted of 'two layers ... held together by liquid'. This was no 'ideal static affair'. In terms of stability - Lawrence's express concern – this meant factoring in the 'mutual effects of the individuality of any one molecule'. And although it invited 'a rigid static conception', Lawrence offered a 'picture' nonetheless. [217]

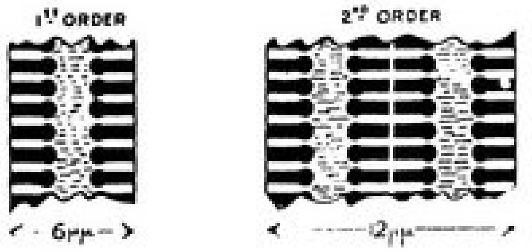

FIG. 59.—Sectional view of black film, diagrammatic.

Figure 13: The 'black'. Sandwich model, 1929

The theoretical rationale for sandwich structures one found in the science of soaps: a matter of orientation, arrangements, adsorbed layers, and the mutual attractions and repulsion among polar (shown as circles) and non-polar groups of molecules. This knowledge was transmitted, notably, by such an authoritative 'discussion of soap molecules'

[217] Lawrence (1929): pp..126-128; p.132.

as could be found in Adam's *Physics and Chemistry of Surfaces,* a text Danielli knew by heart.[218] This 'final black stage' of a soap film, here one learnt, surprisingly enough, was 'the most stable state of the film'.[219] Adam's *Surfaces,* in turn, drew heavily on Lawrence's exposition of soap-stability, reproducing the very same picture of this 'probable structure':

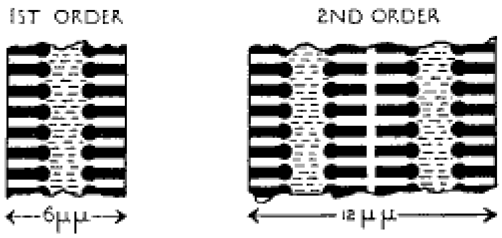

FIG. 28.

Figure 14: The 'black'. Sandwich model, 1930

Danielli, in making the case for his model, simply followed the common wisdom when detailing how the most important properties in stabilizing a soap film, were first, the 'strong orienting and anchoring' tendencies due to polar groups, and second, the mutual attraction of the non-polar parts. And on this basis, Danielli argued, it had to be assumed that the structure of the cellular membrane would be such an arrangement of two layers as well, the only difference being that in the case of the cellular membrane, the polar groups – the adsorbed proteins - would face not inwards, but outwards. It was, or so the science of soap bubbles certainly suggested, such arrangements which rendered the 'anchoring ... most effective'.[220] When it came to films, it was stability that mattered. And soaps, as Adam said, had a 'miraculous power in this direction'.[221]

218 Danielli (1936): pp. 395-396.
219 Adam (1930): p.137.
220 Danielli (1936).
221 Adam (1930): pp.134-138.

Conclusions

Materials, this chapter has shown, whether soaps or nitrocellulose, were a powerful agent mediating knowledge and practices that formed around, and formed, the cell surface: Natural knowledge as a question of ersatz, and artificiality. The bi-layer model, and its material contexts, provided only one, and perhaps unexpected example for such mediation, even though it clearly lacked the mimetic explicitness that characterized much of the earlier modeling practices. But one certainly would not have guessed these entanglements from the title of Danielli and Davson's best known and most influential work: *The Permeability of Natural Membranes* (1943).[222] Republished in 1952, *Natural Membranes* was the culmination the collaboration that ensued between Danielli and Davson in earnest after 1935. Widely greeted at the time as a 'valuable summary of facts and principles' and the first 'general' book on the subject for more than a decade, *Natural Membranes* was an extended argument for the bi-layer model of the cell-membrane, and thus for a particular image of the cell: essentially, a thin, spherical film.[223] Its imagery remains with us until today.

But as such, this chapter has shown, these *Natural Membranes* were a matter of artificiality. They were accompanied, surrounded and built on a plethora of practices centring on a tremendous variety of ersatz-objects, both organic and non-organic: processed *materials*. From filters to leathers to frozen meat to lubrication films and vitamin irradiation products, the micro-dimensions of the cell that were uncovered were not only, or even in the first place, a matter of *natural science*. Nor was this cellular microcosm a matter exactly of molecules or of the well-known, abstract stick-and-balls models, which one felt so absolutely necessary to devise, as William Bragg then explained it in 1925, in a lecture *Concerning the Nature of Things*. '[B]ecause we do not see with sufficient clearness' otherwise he told a youthful audience.[224]

222 Davson and Danielli (1943).
223 See Newton Harvey's foreword to Davson and Danielli (1943); and (1944): p.405; Bennet-Clark (1944).
224 Bragg (1925): p.11; and see esp. Francoeur (1997); Francoeur and Segal (2004); Meinel (2004).

True. Model-experiments were crucial for precisely this reason. But beyond this epistemic surface, even the most esoteric culmination of interwar membrane science, the bimolecular model, formed part of a concrete, material world, as this chapter has shown. Representations of the microscopic were quite secondary to its mundane, palpable substrate and the knowledge embodied therein. Cell-models, manufactured from this substrate, shaped what there could be known about bioelectrical and cellular phenomena, and how it was known: a system of surfaces.

This image of the cell, like the omnipresence of surfaces and substitution materials, was a pervasive vision.[225] And the very artificiality and materiality of interwar life-worlds were of signal importance in mediating it. On the account presented in this chapter, artificiality, control, and mechanism are elements drastically more common - and integral to biological practice - than what is usually assumed in the historiography. Here, all this owed much to the common investigations into 'everyday' materials and products as were exemplified, notably, by colloid science; and it owed little to the usual suspects, philosophical convictions and figures such as Loeb or the Frenchman Leduc, whose *The Mechanism of Life* (1911) reportedly stirred up much (vitalist) sentiments with his artificial re-creations of the living. 'Synthetic biology', to use Leduc's evocative label, was driven by the things themselves, by surfaces:[226] a physico-chemical biology was integral to these mundane practices and sciences of stuff.

Certainly, this was a frequently confused and heterogeneous set of actors, sites and practices, but none that should be judged according to the standards of coherence of a future, potential academic discipline. Neither was this simply a 'dark age of biocolloidity', or the reflections of some 'romantic', holistic *Lebensphilosophie*.[227] On the contrary, in this period, and on very broad scale, as we have seen, complex materials became more

[225] E.g. McClendon (1917); Michaelis (1927); Heilbrunn (1928); Steel (1928); Burns (1929); Michaelis and Rona (1930); Wishart (1931); Findlay (1931).
[226] See Leduc (1911); on Leduc, see esp. Fox-Keller (2002).
[227] Florkin (1972): p.279; Lindner (2000).

transparent, and so did - mediated through ersatz-objects - the cell surface. But seeing this required pursuing the materials of cell-models into obscure, undisciplined landscapes of biological knowing. And there were, as the remaining chapters will explore, other such landscapes, and thus, other models and more dimensions of cellular behaviour. The substrate of cellular life was made-up and mundane; like everyday life, it was not, however, homogeneous.

(2) ENERGY.

Nerve, muscles, and athletes in times of efficient living.

> *Muscular exercise ... Like cosmic rays and solar eclipses this subject gives much satisfaction to the adventurous investigator. The fields of sport and of war, the factory and the farm, the desert, the jungle and the mountains offer tempting problems. ... It is not surprising, therefore, that interest in the physiology of muscular activity is world-wide.* [228]

Early morning on Easter Sunday, 1926: a basement laboratory at University College London, in close vicinity to Euston Station - a buzzing place most of the time... And though it is perhaps hidden, as so often, behind a 'smoke-befouled atmosphere', Metropolitan London, the 'ringleader' of modern, urban life, is still asleep. It is, generally, a disconcerting, unnatural environment, or so, at least, go the complaints; here the people, if we believe the keen-eyed, more sinister observers, go about their daily business 'in basements or corridors, in trams and tubes, in the stabbing glare of theatres and restaurants, ... straining to high desks, stooping to low desks, hunched on stools; receiving dim daylight at one angle through an inadequate window and the cast shadows of ill-assorted artificial lights that send their wasteful rays in every direction but the right one.'[229] But today, no doubt, is a day when 'the public' is 'attentive to other matters than daily life, and we [scientists] usually try to get a bit of research work done'.[230]

There is indeed a delicate high-precision measurement experiment underway under the ever-critical gaze of the famed biophysicist A.V. Hill; age: forty, tall, athletic, slightly tanned, a dashing, slim moustache, alert as always, just recently having been appointed

[228] Dill (1936): p.263.
[229] Leonard Hill (1925): p.iii, p. 46; Sinclair (1937): pp.41-42.
[230] So went an appreciation letter from Harvard. See Parker to Hill, 10 May 1926, AVHL II 4/66

Foulerton Research Professor of the Royal Society. Hill's personal mechanic, A.C. Downing, stands by his side, closely observing the complex arrangement of iron-wire-cages, solid shields fabricated from the alloy *Mumetal* (courtesy of the Gutta Percha Company, London), a series of Downing's much acclaimed galvanometers, everything stacked on top of a three-ton pillar dug into the solid ground underneath the College. Also with them in this unholy hour is the young physiologist Ralph Gerard, a post-doctoral visitor from Chicago.

The city is still quiet enough to let the experiment begin. It is a historic moment in the history of the nervous impulse: in what is a truly 'remarkable achievement in the field of physiology', or so the *Lancet* will comment, Hill and his collaborators go on to show that a nerve seems to behave, surprisingly, almost like a little twitching muscle – albeit, on an much smaller scale: 'per impulse', these Easter experiments suggest, nerve liberates about the millionth part of the energy liberated per single muscle twitch. Or 0,000069 calories per gram per second; 'excessively small', as they say, disturbingly close to nothing.[231]

This scene introduces the biophysical enterprise - a resource-intensive, high-tech venture - that is the subject of the present chapter. The theme is not material *ersatz* but technical and conceptual *transfer* among and between living, natural phenomena. Transfer from muscular to nervous activity, to be precise, and this will crucially involve energetic conversions, heat liberations, and even the whole, athletic human body - 'fearfully and wonderfully made' as Hill often enthused.[232] This chapter, accordingly, will lead us away from colloidal phenomena, materials and membranes and on to another set of modern, industrial sciences relative to which, I shall argue, the cell gained substance in the interwar period: the burgeoning physiologies of work, exercise, and sports. Like the previous chapter, this one too will be concerned with the ways the elusive nature of bioelectrical

[231] A.V. Hill (1926a): p.163; nn. (1926b): p.866.
[232] A.V. Hill (1933c): p.324.

activity was given shape and assumed concrete reality. And it too will approach the question through the interwovenness of models, phenomena, scientific practices and scientists' modern, industrial life-worlds. Only the *substrate* differs: less ostensibly and overtly, I shall argue, mediated through concrete acts of transfer – of techniques, of instruments, of entire experimental systems – as far as cellular behaviour was concerned, muscular activity in general, and the athletic, neuro-muscular body, in particular, accrued biological model-function. The special behaviour at issue was the fundamental nature of nervous activity.

Around 1930, as this chapter shows, this elusive nature had taken fragile, uncertain shape as an energetic event - the presumably fundamental complement to the (historically) more familiar, electrical, signature of the nerve impulse. It is a story revolving around the absence or presence of a delicate outburst of heat production that will concern us here: the excessively small outburst first making a registrable appearance in the records on the Easter Sunday of 1926. And it is, as such, an account of the physiological model-phenomena that rendered this outburst real. This uncertain event and with it, a particular image of nerve as a heat-producing, and thus muscle-like, energetic phenomenon, was given shape and made real, I shall argue, at the margins of a muscle-centred science, mediated through its applications to man. In the scene above was emerging a peculiar incarnation of the nervous impulse – an impulse modelled on muscular activity and moving bodies.

Exposing this model-function also means to re-align the history of nervous behaviour with a broader, cultural history of the interwar period, and a history of the body in particular. Above enterprise indeed did not revolve around twitching, isolated muscles only, but formed part, as we shall see, of a much broader set of useful investigations into the whole, neuromuscular body. This, to be sure, is to invoke a rather cliché historical image - but one that will serve its good purposes here. More generally, of course, from the (British) Sunlight League to mushrooming sports club to the sciences of industrial health and efficiency, bodies then were a serious matter of concern. The resulting picture of this muscle-like nerve cell indeed will not mesh very well with our contemporary, brain-and-mind-centred intuitions of what this history was all about. What these brain-centred narratives obscure is precisely what will be of central importance here, the crucial scientific and cultural significance of the peripheral nervous system: the much more palpable, familiar and intensely studied phenomena of muscular activity, bodily motion and athletic exercise.

It was in virtue of being the objects of this intense, pervasive interest that they came to mediate physiological knowledge of the nerve impulse. This indeed was mundane knowledge, esoteric only in its finer details. The 'chief' waste-product of muscles in activity, treatises such as *Athletics* (1929), a joint production of the Cambridge and Oxford University Athletic Associations, explained - this one along with some helpful hints in this connection by Hill on achieving 'economical results' when running -, was 'lactic acid and it is this substance which is responsible for the feeling known as fatigue.' And all these were phenomena of utmost complexity.[233] The long-held notion according to which the contractile action of muscle could to be conceived of in terms of a simple (and aerobic) *combustion* motor had long fallen victim to scientific progress, as the director of the Kaiser-Wilhelms-Institut für Arbeitsphysiologie concurred. A product of the nineteenth century, in 1930 it was a trope carrying not much weight any longer.[234]

The body in question was not a brute heat engine, as we shall see. Athletic and healthy, it was a subtle, complex machinery, a matter of posture control and neuromuscular coordination. Unlike the raw, muscular machinery that populated nineteenth century factories and imaginations, this machinery articulated itself in terms of bodily skills and complicated movements.[235] Its energetic efficiency was - so went the upshot of a decade of

[233] Lowe and Porritt (1929): pp.106-107.
[234] Atzler (1930): p.20; also see Elliott (1933); A.V. Hill (1924a).
[235] Esp. Rabinbach (1992); Sarasin and Tanner (eds.) (1998).

researches at Hill's London Biophysics Research Unit above - determined primarily by the 'economy ("skill") with which [its energy] is used'.[236]

In the following account such unlikely partners as modern cities, dexterous athletes, crabs, rural idyll, muscular skill and the nervous impulse itself become intimately entangled in a realm of *analogical* phenomena. Their coming together was crucial, I argue, to the production of authenticity and 'genuine' physiological effects, and thus, to rendering what seemed to many as little more than an artificial laboratory product of dubious existence into a genuine, physiological event. And accordingly, the following will turn out to be a more complex story than one of early mornings, advanced technology, and the vagaries of urban experimentation.[237] True nature, as we shall see, was not easily exposed in central London, not even on an Easter Sunday. No question, as Hill, Downing, and Gerard complained, barely concealing their frustrations with the urban life, the limits of precision measurement could have been pushed further 'in a quiet laboratory in the country'.[238]

But here they were, in their urban, artificial surroundings, establishing, on this Easter Sunday, for the first time in history what seemed conclusive evidence that heat was being liberated in nerve during activity. Meanwhile, outside, the city is just coming back to life: underground and overground, trains, trams, the tube, cars, people begin to traffic and move; mechanic vibrations ensue that disturb the experimental silence. And it resume the all-pervasive electromagnetic interferences that emanate from broadcast stations, domestic wiring and the overland cables that cover the city like spider-webs. Hence the pillar, hence the shields; hence early mornings, or late-nights, preferably on weekends – only on 'special occasion[s]' does this hostile environment allow for high-precision measurement practice.[239]

236 HMSO (1927): p.15.

237 On the vagaries of urban, physiological experimentation especially, see Dierig (2006); Felsch (2007); also see Schmidgen (2003); Agar (2002).

238 Downing, Gerard, and A.V. Hill (1926): pp. 231-233.

239 Ibid., p.230.

The physiology of modern conditions

The 'physiology of isolated muscle', A.V. Hill was confident, 'is already able to illustrate and explain many of the phenomena associated with athletics, physical training, mountaineering, dypnoea, and other phenomena associated, in health and disease, with bodily movement and effort.'[240] The year is 1923, and here we have Hill reporting to the Medical Research Council of his ongoing investigations in *applied physiology*. Hill had begun to pursue investigations of this kind on behalf of the Council's *Industrial Fatigue Research Board* (IFRB) some three years earlier, in 1920, the year Hill, himself a product of the famed Cambridge School of Physiology, was appointed to the newly created chair of physiology at the University of Manchester.[241]

At the young age of 34 Hill had become the first Professor of Physiology at a British university without a medical qualification. Hill nonetheless was deeply concerned about bodies. Most notably so, it was the 'oxygen consumption during running' which Hill at the time begun to elucidate, together with the assistance of a young Manchester physicist, Hartley Lupton ('never so happy as when "going all out"').[242] It was a pursuit devised to expose the fundamental physiology of isolated muscle in the whole man. The phenomena, in turn, that were here being uncovered would quite certainly be of service, as Hill commended his investigations, also 'to those concerned with man as a living unit in a social and industrial system'.[243] At any rate, they would, as will become clearer in due course, serve to expand the truths of the physiology of isolated muscle into the real, natural, lived world - well beyond the laboratory, that was, and the world of isolated frog's muscle. And what will concern us even more, this lived world would eventually return on

[240] Hill, 'The Physiology Department: The University: Manchester' (report 1923), FD 1/1948

[241] Hill, 'The Physiology Department: The University: Manchester' (report 1923), FD 1/1948 ; on the Cambridge School, see esp. Geison (1978); Weatherall (2000); Tierney (2002): chapter 3.

[242] A.V. Hill and Lupton (1922); on Lupton, see A.V. Hill (1960a): pp.124-143.

[243] Hill, 'The Physiology Department: The University: Manchester' (report 1923), FD 1/1948

the level of isolated organs and tissues: nervous activity, to put the argument-to-follow crudely but succinctly, was by proxy fabricated as a matter of going all out: fatigue, exhaustion, and in extreme conditions - severely *exercised*.[244]

It was 1920, as Hill was entering a new, post-war life in physiology, that marked what was the beginning of Hill's distinguished career as an authority of applied physiology - somewhat unfitting, or so it might seem, for this acclaimed pioneer of academic biophysics.[245] But the impression is quite wrong. This Cambridge *Wrangler*-turned-biophysicist, Nobel prize winner in physiology and medicine (1922), veteran of anti-aircraft gunnery, and indeed, noted pioneer of the physiology of sports, was deeply enmeshed, this chapter shows, in this much vaster and useful project of physiological application. Long before the elusive manifestations of nervous heat would become manifest, in the hands of Hill and his scientific allies *athletic machinery* already had begun to yield a life-size image of intricate, energetic processes. We should not be too surprised - 'After World War I', as Gerard would later diagnose of his chosen metier, 'popular demand ... ha[d] reinforced the popular notion limiting physiology to its application relative to the functioning human body.'[246]

In Britain as elsewhere, it is true, the Great War had had a significant impact on physiology as a profession, its organization, its uses (of which there were many), its outlook, import and sheer scale.[247] One of the more visible expressions of these new horizons, the IFRB above, like the MRC itself, had been among the products of the recent carnage, originating in the war-time *Health of Munitions Workers Committee* (of the Ministry of Munitions); post-war, the Board quickly ascended to something of a pet project of the

[244] Not coincidentally, terms such as 'exercise', 'performance', or 'efficiency' were routinely used to articulate the behaviour of isolated organs.

[245] Though Hill, the physiologist, has not received much historical attention, it is the picture of pioneer that dominates the historical record, see esp. Katz (1978); Tierney (2002); Chadarevian (2002).

[246] Gerard (1958): p.199.

[247] Little systematic work has been done on these developments. Some sense of these shifts is conveyed by Franklin (1938); Veith (ed.) (1954); Rothschuh and A. Schaefer (1955); Gerard (1958); also see Howell (1985); Sturdy (1992a); Sturdy (1998).

MRC's newly minted secretary, Walter Morley Fletcher, himself a Cambridge man and muscle physiologist.[248]

The war, as Fletcher, who also had been Hill's tutor and fatherly friend at Trinity College, Cambridge, would diagnose in 1926 had 'brought into sharp relief our ignorance of the general physiology and psychology of work.'[249] It was a serious legacy. Here one dealt with a matter of strategic urgency, a question of economic efficiency, and not least, therefore, with the health of the nation - the 'fitness and the physique and the beauty', that meant according to Fletcher, 'of men and women in their prime.'[250]

As Fletcher admitted on the occasion (and as historians have explored) labouring bodies, fatiguing bodies, thermodynamics, industry and energy had, of course, long troubled physiologists.[251] In this respect the nineteenth century bias of the historiography, however, can be misleading. Muscular energetics had its roots in the nineteenth century, arguably the age of energy and thermodynamics, but it does not fundamentally belong there. In the nineteenth century, it was a set of discourses, as Anson Rabinbach's *Human Motor* in fact rightly has stressed, that had materialized around a concept – physiological fatigue – and a number of scientific novelties that ranged from the chronophotographic motion studies of Marey and Muybridge to the nutrition experiments of a Rubner and Mosso's heroic physiology of alpine mountaineering.[252] It was in the far less richly explored interwar period that the applications of physiology to industrial life gradually were transforming from pioneering, exotic effort into a matter of routine. This is crucial to keep in mind here; not least because it was this relatively pervasive, mundane pursuit of the physiology of muscular activity that will allow construing its model-function in terms not unlike the everyday ontology of fabricated, synthetic materials and surfaces. Muscular

248 M. Fletcher (1957): esp. pp.338-339; A. Landsborough Thomson (1978); Austoker and Bryder (eds.) (1989).
249 Fletcher, 'The growing opportunities of medicine', 1926, copy in AVHL II 4/27
250 Fletcher (1928), cited in M. Fletcher (1957): p.237.
251 Rabinbach (1992); also see Sarasin and Tanner (eds.) (1998); Felsch (2007).
252 again see esp. Rabinbach (1992); Gillespie (1987); Gillespie (1991); Vatin (1998); also see Braun (1992); B. Clarke (2001); Clarke and Henderson (eds.) (2002).

activity was similarly palpable, indeed familiar.

It is important not to confuse the rise and demise of what may have been a fatigue/energy discourse specific to this earlier period with a demise of the physiology of work and sports. The latter, like the pursuit of sports by the masses itself, coalesced and expanded in the interwar period in particular.[253] For many of the countless, nameless heirs of these nineteenth-century, physiological icons, and for the likes of Hill or his influential friend Fletcher as well, the narrow concept of physiological fatigue, the *human motor* crudely conceived as a heat-engine and the merely superficial tracings of the outwards appearance of bodily manifestations as curves had indeed been losing much of their initial appeal. The problem these interwar students of muscular activity encountered was a much wider, more fundamental, total one. For them, men 'living in submarines below the sea, mining far into the earth, or flying to great heights in the air' - so Fletcher's own list of contemporary, physiological extreme-situations went - only exemplified what was a general, and fundamentally biological problematic of living in modern, artificial surroundings.[254] If there was an energetic discourse here, it was not informed by heavy labour, factories and the threat of depletion and fatigue, but the notion that any type of movement and manoeuvre in modern, artificial environments equalled a sportive act: a matter of extreme performance. 'Did you ever carry in your motor car', Hill inquired with Fletcher in 1926 en route towards his new little summer house in vicinity of the Plymouth Marine Biological Station (more on which later), 'three adults, four children, one dog, four large suitcases, one small ditto, one bed, one cricket bat, one umbrella, for 140 miles at an average speed of 29 miles per hour...?'[255]

The 'relative suddenness of the industrial revolution', as the historic circumstances presented themselves to the MRC secretary (himself renowned for his 'strength of body

253 Here, the literature is less extensive, but see Winter (1980); H. Jones (1989); Chapman (1990); Schneider (1991); Heim (2003); J.K. Alexander (2006a); J.K. Alexander (2006b).

254 See W.M. Fletcher (1932a): pp.190-192; also see W.M. Fletcher (1932b); W.M. Fletcher (1931).

255 Hill to Fletcher, 23 April 1926, FD 1/1818; also see Hill to Fletcher, 27 September 1926, FD 1/1948

and quickness in all forms of sports') 'ha[d] produced problems of industrial life and city life for which we are unprepared.' And these, he said, were 'really problems of physiology'.[256] In this encompassing and optimistic vision of biology, there was nothing unusual about Fletcher as much as Hill would be badly construed, as we shall see, as the exceptional biophysical pioneer; both were typical, indeed almost stereotypical interwar figures (albeit ones atypically influential). In the aftermath of the war, intersecting with shifting perceptions of Nature, fitness, health, and leisure, and accompanied by an exploding popular literature that promoted an enhanced knowledge of one's own body and biology, the expanding stretch of physiological science to many a scientist (and non-scientist too) seemed inevitable.[257] Not least, it seemed inevitable in relation to the industrial life where performance was a question of both, labour and leisure. Journals such as *Arbeitsphysiologie* or *Le Travail Humain* were first launched in the late 1920s; in parallel, centres such as the Kaiser-Wilhelms Institut für Arbeitsphysiologie in Dortmund, the laboratory for the *Theory of Gymnastics* in Copenhagen, and departments of work and exercise physiology in the U.S., Britain, Sweden, France, Russia and Japan came into existence.[258] Cambridge physiologists would travel the Andes and Nazi scientists the Himalayas; aviation physiology came into its own, and so did the physiology of sports; ergonomic design entered the factories, schools and offices.[259] Athletes, both professional and amateur, paid closer, and scientific attention to the appropriateness of diet, training, and dress; meanwhile, physiologists lost no time investigating scientifically the sportive phenomena that were to be witnessed by the masses at the Olympic Games in Amsterdam (1928), Los Angeles (1932) or Berlin (1936); and the large-scale Soviet efforts in the

[256] Fletcher, 'The growing opportunities of medicine', 1926, copy of MS in AVHL II 4/27; Fletcher (1928), quoted in M. Fletcher (1957): p.236; Elliott (1933): pp.152-154; Fletcher (1957): p.236; Elliott (1933): pp.152-154.

[257] See e.g. H.G. Wells, Julian Huxley, and G.P. Wells (1929); Hogben (1930); Crowther (ed.)(1933); Adams (ed.) (1933); J.A. Thomson (1934); and see Mazumdar (1992); Lawrence and Mayer (eds.) (2000); Stone (2002); Zweiniger-Bargielowska (2006); Vernon (2007); Overy (2009): esp. chapter 4.

[258] E.g. Atzler (1929); Newsholme and Kingsbury (1934); Crowther (1936); Dill (1936): pp.263-264.

[259] E.g. Franklin (1953); J.K. Alexander (2006a); Phillips Mackowski (2006); Hoebusch (2007).

applications of physiology in particular filled Western observers, including Hill, with envy and awe.[260]

As a great deal of historical work on the period has shown, this heterogeneous, but intensely felt excitement revolving around the body stretched from physical culture and outdoor grass-roots movements to the technocratic discourses of national efficiency and rationalization. It was reflected in the arts, straddling left and right, neo-romantic and avant-garde, conservative and progressive, as much as it began to shape personal behaviour, labour relations and economic policies.[261] And no-one, to be sure, could blame the Britons with idleness.

The IFRB, in particular, of whose *Committee on the Physiology of Muscular Work* Hill had been a member from its inception, was a venture of international acclaim; its mission laudable and timely. Renamed the *Industrial Health Research Board* in 1928, it was to tackle the physiology and psychology of man's 'industrial surroundings' in its entirety: heat, noise, atmospheric conditions, light, dust, the design, and the 'bodily and mental adaptation' to machines. In the grand scheme of the IFRB, industrial health and efficiency was a complex, multi-faceted, and multi-causal phenomenon.[262] By 1928, researches on behalf of the MRC as Fletcher triumphantly reported, were on the verge of discovering the 'conditions of work that give optimum ease and efficiency in its performance'; and even, of 'exposing the penalties we pay in health for the pall of smoke that we allow to hang over our great cities, and revealing the true values and use of sunlight.'[263] Hill's own investigations occupied a prominent place among them. In 1931, the *Lancet*, in a survey of the state of the 'Science of Exercise' in England, thus was able to take pride not least in the 'fascinating experiments with Human Machinery' by Hill and his (by then) numerous co-workers: the 'liberality with which these British workers are quoted', one read, 'is ample testimony to the

[260] A.V. Hill and McKeen Cattell (1935); Solandt (1935); also see S. Gross Solomon (2002).
[261] On this protean nature, see esp. J.J. Matthews (1990); Mackenzie (1999).
[262] See the annual reports of the Board, esp. HMSO (1931): esp. pp.4-5; pp.75-77.
[263] Fletcher (1928) cited in M. Fletcher (1957): pp.236-237.

authority with which their results are invested.'[264]

The muscular science of A.V. Hill

By the time of Easter Sunday 1926, as physiologist-philosopher A.D. Ritchie surmised in his *Comparative Physiology of Muscular Tissue* (1928), Hill and his colleagues already had made this 'particular branch' of physiological science 'almost entirely their own'.[265] This was hardly an exaggeration. Hill had long emerged as the unchallenged authority in the field of muscular energetics, a master of experimentation dominating its fundamental, biophysical aspects as well as its applications to man-in-motion - notably, as Hill said, to the 'records of athletics and sports'.[266]

And by the time too, there had long been crafted a definite, fundamental picture of muscular activity. Here one may well have dealt, as Lancelot Hogben opined in 1930, with one of the most 'outstanding developments in biological research' of recent. It certainly was, or so he surmised, the only one which 'represent[ed] an advance in the actual reduction of vital processes to physical chemistry'.[267]

It was in particular, so Hill had surmised in 1920, the 'incomparably greater accuracy and speed' of biophysical instrumentation that has lead, over the last few years, to profound advances as regards our knowledge of muscle.[268] Hill had in mind here the so-called thermo-electric methods in particular, and thus, his core field of expertise: extremely delicate and sensitive techniques that allowed recording the heat given off by living, intact muscle and the like. Biochemical methods, as were mastered notably by Hill's scientific ally Otto Meyerhof in Germany, in contrast, invariably were destructive, and thus, the common

[264] nn. (1932a).
[265] Ritchie (1928): p.59.
[266] A.V. Hill (1925); on Hill, see Katz (1978); Tierney (2002); Bassett (2002).
[267] Hogben (1930): p.35.
[268] A.V. Hill and Hartree (1920): p.122.

perception went, incapable of charting the temporal process-nature of living phenomena: they were analyses, for the most, of mashed up muscle - *Muskelbrei.*[269]

Muscular activity, an unquestionably biochemical, energy-consuming process, the biophysical wisdom suggested, resolved into a sequence of several *phases*: contraction, relaxation, fatigue, and restoration. Each phase, as Hill had begun to precisely establish in the 1910s just barely having graduated, was associated with a definite and appreciable amount of heat being liberated, and thus, each with a chemical process of some kind. Subject to continual tinkering and improvement, by the 1920s there had emerged a complex, soon routinised sequence of interventions and record-analyses that led from data production to physiological meaning. The distinctive, diagrammatic end-product, a kind of bar chart, typically looked like this:

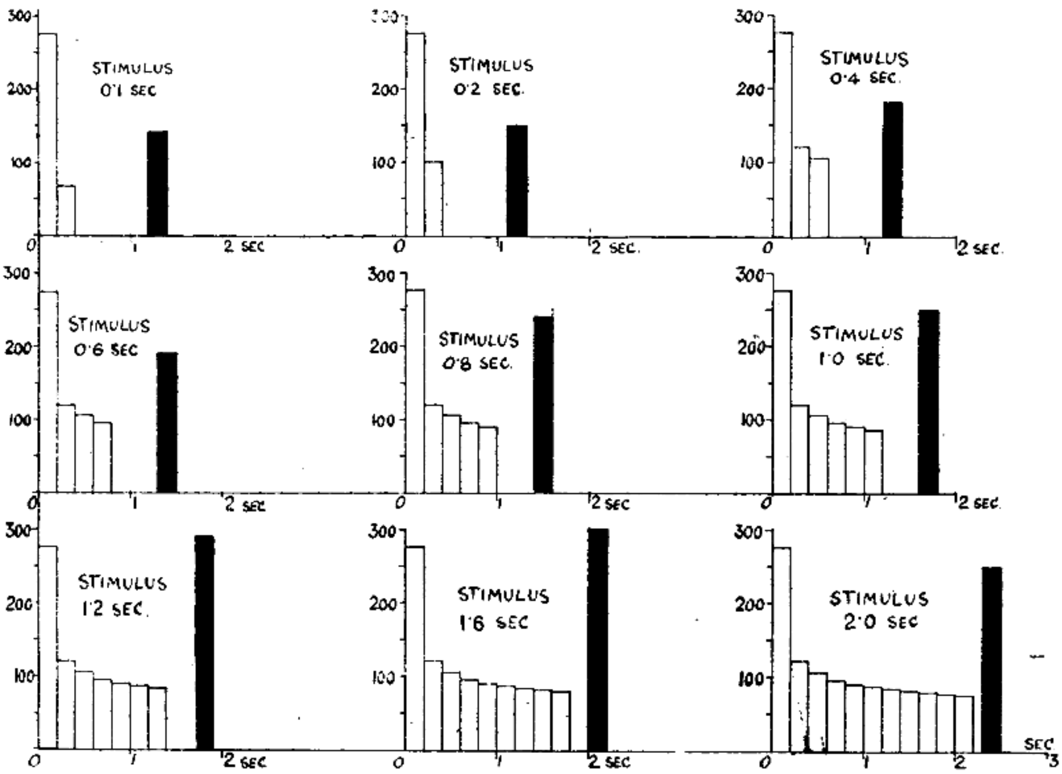

Figure 15: phases of muscular heat production, 1920

[269] On Meyerhof, see Peters (1954); more generally, the best source is Needham (1971).

So looked the science that won Hill a Nobel-prize, jointly awarded in 1922 to Hill and the German Meyerhof – a significant gesture, certainly on Hill's mind, of reconciliation in the 'international brotherhood' of physiological science.[270] And according to the vision of muscular activity they stood for, the so-called Hill-Meyerhof theory or lactic-acid theory, the contractile process of muscle involved essentially, the – entirely anaerobic - formation of lactic acid first (contraction), followed by its 'oxygenative disappearance' (restoration), an energy-consuming process preventing – within definite limits - the accumulation of lactic acid.[271]

The origins of this hugely influential vision - a vision irreconcilable with the cherished analogy between muscular activity and (aerobic) oxygen-combustion motors - dated back to the 1900s, and another basement laboratory. This one was located in the far more idyllic Cambridge, a site that profoundly shaped Hill as a scientist: the legendary, damp 'cellar' of the Physiological Laboratory where Hill learned his trade working alongside such other eminent figures as E.D. Adrian, Keith Lucas, John Langley, Joseph Barcroft, Walter Morley Fletcher, and Frederick Hopkins. In terms of physiological science, this was perhaps the most exciting place to be at the time. The *Cambridge School* of physiology was then unquestionably emerging as the avant-garde of physiological science.[272] Lucas, a celebrated designer of instruments, was pushing the electrical analysis of the nerve impulse towards new and quantitative horizons by way of precisely timed currents; Langley was in the process of formulating the all-important concept of 'receptive substances'; meanwhile, Fletcher, Hill's tutor at Trinity College and the future secretary of the MRC, was laying the foundations, together with the biochemist Hopkins, of the anaerobic theory of muscular contraction - the subject Hill and Meyerhof would soon take

[270] A.V. Hill (1925): p.486; to get a sense of Hill's strong convictions, see A.V. Hill (1929b); A.V. Hill (1960b); also see Zimmerman (2006).
[271] E.g. A.V. Hill (1927a); Ritchie (1928); Meyerhof (1930).
[272] H.H. Turner (1934); See A.V. Hill (1965); on the early history of the 'school', see Geison (1978); also see, Weatherall (2000); Weatherall and Kamminga (1992); Tierney (2002).

over.[273]

Fletcher and Hopkins, for their part, had joined forces in 1905, studying the presence of lactic acid during the various 'physiological phases' in isolated frog muscle. Soon, the two had established very definite evidence for the 'oxygenative disappearance' of lactic acid during muscular recovery. And more iconoclastic, these results - obtained by respiratory methods - suggested that the contractile phase – muscle action - was not motor-like at all but involved a purely anaerobic process of lactic acid formation: oxidative processes entirely concerned the aftermath: 'recovery' processes.[274]

'[B]arely rooms at all', here one was surrounded by fundamental advances and achievement; painstaking, patient observation; an empiricist ethos of perfection and little time for speculation. Lucas in particular, as Fletcher recalled in awe, 'could not respect that which he did not prove. I think this is all. Prove *all* things, ALL THINGS. Hold fast that which is good.'[275] Cambridge was a special place at the time also in so far as training there in *physiological science* operated largely and deliberately independent of the requirements of a medical school. Organizationally, it formed part of the Natural Sciences Tripos.[276] Students typically read combinations of three to up to five subjects – then including physics, mathematics, chemistry, botany, zoology, physiology, geological sciences, anatomy, and pathology. Only in part II of the Tripos they were to pursue more specialized studies. Such were the 'Cambridge traditions', and, so influential circles tended to believe, this was the main 'educational advantage of residence in Cambridge.'[277] It was unique an experience, certainly different from the physiological education to be had in London, Oxford, Liverpool, Sheffield, at Harvard or at one of the German universities. Tea-rooms, the 'Cambridge system of 'prize fellowships'', and the 'hard discipline' instilled by a proper

273 On Langley, also see Maehle (2004); on Fletcher, see M. Fletcher (1957); Austoker (1989); on Hopkins, see esp. Weatherall and Kamminga (1996); on Adrian, see Frank (1994).
274 Elliott (1933): p.157; Needham (1971): pp.33-42.
275 A.V. Hill (1965): pp.4-5; Fletcher in H.H. Turner (1934): p.72.
276 Weatherall (2000); esp. H. Blackman (2007).
277 Medical Science Tripos Committee Minutes (1930), p.19, CUL/University/Min.V.75; 'Report of the Syndicate on the Medical Courses and Examinations' (June 1932), ROUGHTON/APS, Box 34.60u

training in 'exact methods', Hill will venture, were the secrets behind the great achievements of Cambridge physiology.[278]

And Hill, evidently enough, was no average physiological student. Hill, Fletcher's most notable recruit to physiology, was a product originally of the famous Mathematical Tripos, drilled in the formal discipline by the theoretical mathematician G.H. Hardy. In 1905, a 'very hot year', Hill even had finished as Third Wrangler, and only then, under the guidance of his tutor, Fletcher, Hill switched over to physiology, chemistry, and physics, taking a first in physiology in part II of the Natural Sciences Tripos in 1909.[279] By 1913, he had been appointed to a readership in Physical Chemistry impressing his fellow physiologists, young and old, with 'advanced courses' in the subject. And it was then, in the late 1900s, that John Langley, the Cambridge Professor of Physiology, had advised Hill to 'settle down to investigate the efficiency of cut-out frog's muscle as a thermodynamic machine'.[280] Langley also furnished Hill with his first galvanometer-thermopile combination, a so-called Blix galvanometer – Hill's entry into the fundamental biophysics of muscle.

'All sorts of external disturbances would act upon it', Hill complained in his very first publication on the subject, but the basic principle was simple enough: thermopiles - delicate, bimetallic circuit-elements - convert changes of temperature – those accompanying a twitching muscle, for instance - into an electric current.[281] With the knowledgeable assistance of the *Cambridge Scientific Instrument Company*, whose richly illustrated trade catalogues then were a vivid confirmation of the 'great progress' of recent in the science of thermometry, Hill would patiently coax the fickle device into operation. 'In many processes', as a Company brochure read, 'where the judgement was previously determined by the eye of the workman or in some equally vague and deceptive manner,

278 See Hill to Fletcher, 7 May 1929, FD 1/1949; Hill quoted in Flexner (1930): p.260; and Crowther (1970): p.175.
279 Fletcher to Lovatt Evans, 17 June 1929, FD 1/1949
280 See letter Langley to Hill, November 1909, quoted in A.V. Hill (1965): p.4.
281 A.V. Hill (1910): pp.390-392.

thermometers are now in regular use'.[282] Electricity-based methods, replacing mere eyes and vagueness, were the most exacting. In 1911, Hill thus travelled to Germany to be introduced to the higher secrets of electro-thermometry by Friedrich Paschen, the renowned infrared-spectroscopist and future president of the Physikalisch-Technische Reichsanstalt.[283] By 1914, when Fletcher and Hopkins delivered their Croonian Lecture on the ('plainly' anaerobic) 'Nature of Muscular Motion', they could point to the 'valuable series of parallel observations' by Hill derived with the 'most refined thermo-electrical methods'.[284]

Hill, as Fletcher would write, after his Tripos experience had 'definitely wanted to turn to something [else], preferably of a humanitarian kind' - something where his mathematical skills would enter as 'a means and not as an end in itself.'[285] Skills apart, the masculine hardships of the Tripos – meticulously analysed in Warwick's *Masters of Theory* - abstract paper-work, competitive examinations, formal drill and discipline as ends in themselves, no doubt, left deep traces on Hill, the biophysicist.[286] Hill would have little patience with biologists' tendency of being 'woolly-headed and diffuse', persistently defend his subject as a biological science that was also 'intellectual respectable', or indeed, complain how in 'its elementary stages the study of biology provides little of the discipline which we associate with mathematics, or with Latin or Greek. ... there are no difficult things to understand; there are no problems to solve, no examples to set ... The mind like the body', Hill's lesson went, 'can only be trained to best performance by setting it to do what is hard.'[287]

The biophysics of muscle, as Hill imagined it, was indeed conceived in this climate.

[282] CSI (1906): p.1; A.V. Hill (1913): p.28.
[283] Katz (1978): p.81; A.V. Hill (1913): p.28.
[284] W.M. Fletcher and Hopkins (1917): p.456.
[285] Ibid.
[286] Warwick (2003).
[287] Hill (1923), reprinted in A.V. Hill (1960c): pp.16-17; A.V. Hill (1932a): preface; A.V. Hill (1931b): p.21.

It was not only a penchant for formal discipline that had left its traces on Hill. It was in Cambridge where Hill first began to develop his deep and deeply personal (and ideological) commitments to athletic machinery – the object that would come to frame his science. Not perhaps, surprisingly so: Cambridge, as much recent work on its history has shown, was a place not only of science, but one deeply aware of the body: athletics and sports, militarized to various degrees, formed an integral part of the pursuit of the scientific life at Cambridge.[288] Well into the twentieth century students were expected to participate, despite their increasingly crammed time-tables, in 'the normal, social and athletic life of the University and its Colleges' as a University committee demanded it in 1930.[289] Warwick's work on Cambridge mathematical pedagogy in particular has shown how intimately intertwined the abstract mental discipline students were subjected to was with a compensatory, almost obsessive attention to the body and bodily activity. The beer-drinking, unhealthy, unsportive habits of the German students at their renowned research universities were observed with contempt, if not disgust.[290] Hill would be no exception. Visiting Germany in 1911, Hill wrote back to his fatherly friend Fletcher - rather appalled - that he did 'not like the typical German student. He is too fat, ugly, smug and covered with gashes.'[291]

Hill, for his part, was known for having 'always believed in keeping himself fit'. From his earliest student days, as Fletcher approvingly surmised in 1929, Hill had been 'fond of running exercise ... [and] was keen, too, upon his rifle shooting' (a hobby he pursued in the Cambridge Officers' Training Corps).[292] By then a man of considerable stature, Hill would not loose an opportunity to deplore how 'individuals' were generally, and unfortunately, 'ignorant of the wonderful body they possessed'. Most spectacularly this

[288] In addition to Warwick (2003); also see Deslandes (2005); Levsen (2006); Levsen (2008).
[289] Medical Science Tripos Committee Minutes (1930), p.21, CUL/University/Min.V.75
[290]Warwick (2003): chapter 4.
[291] Hill to Fletcher, c.1911, AVHL II 4/27
[292] Fletcher to Lovatt Evans, 17 June 1929, FD 1/1949

happened, perhaps, during Hill's Christmas Lectures at the Royal Institution in 1926.[293]

Published (and reissued several times) as *Living Machinery*, these lectures brought nearer to the young people, by means of 'fearful experiments' and moving pictures, the true workings of the body; and that of muscles ('which move it about') and nerve ('which arrange where and how it shall move') especially. Culminating, almost naturally, in a celebration of *Speed, Strength and Endurance*, they presented an extended argument concerning the 'chief factor' in athletic achievement: the 'supply of energy and its proper and economical utilisation'.[294]

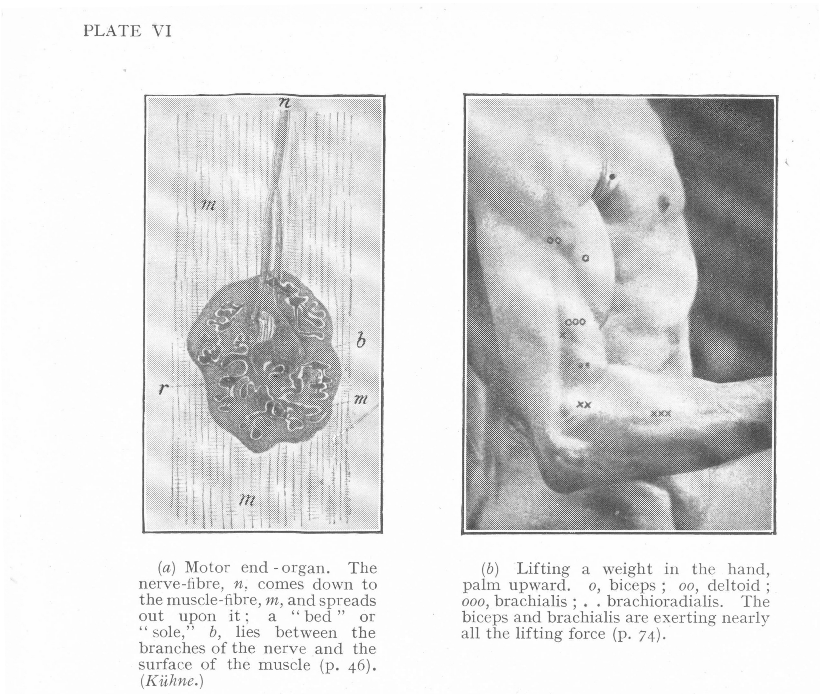

Figure 16: How muscles work, Living Machinery (1927)

In ways going well beyond a compensatory activity, Hill had come to combine his believes, and his personal, athletic existence, with his own scientific pursuit. Indeed, the main thrust of the following is to show just how profoundly the athletic (and industrial) life was endemic in this pioneering and widely acclaimed biophysical enterprise - in more than one, and complexly intersecting, ways.

Examples can be multiplied. Though quick to extol the pure, anti-dogmatism, internationalism, self-discipline and originality as the core values of science (something Hill is better remembered for), Hill thus would come to engage very actively indeed with the

[293] nn. (1926c): p.8; nn. (1926d): p.7.
[294] A.V. Hill (1927b): esp. pp.ix-x; lecture VI.

functioning human body and its uses, lecturing with especial zeal on athletics, man in motion and the 'scientific contemplation' of one's own, personal body.[295] And Hill would, between the wars, be writing on and lobbying for improved education in biology as well; worry about methods of physical education in schools and the army; serve on various Government committees whose terms of reference ranged from the physiology of muscular work, to optimal ventilation and heating in the industry, to 'visibility' studies ('fog and mist', 'dark adaptation', 'illumination factors', 'selection and training') on behalf of the Air Ministry.[296]

The tremendously broad significance of physiological science to almost every aspect of the industrial life was beyond doubt on Hill's scheme of things. Hill may often have enthused about 'the wonder, the beauty, the complexity of life in the scientific sense' that was urgently to be instilled into the average citizen.[297] But his list also included, notably, a great many more practical, and rather less pure items: 'fatigue in men and women; nutrition of workers; heating and cooling; noise, rest-pauses, skill, vision, illumination;...diving ...food preservation ... high flying ... athletic records ... running upstairs ... bicycling...' - so, for instance, he once presented the cause to an audience of engineers.[298]

When it came to the uses of physiological science, Hill was a man of words as well as deeds. Ultimately much more interesting here than Hill's verbal output will be his extensive forays into a physiology of exercise. After all, it was here, in the exploding, hands-on, interwar pursuit of athletics and sports as 'a science and an art' (in Hill's words) where neuromuscular activity could be most intimately felt, experienced, observed.[299] As

[295] A.V. Hill (1925); A.V. Hill (1926b); A.V. Hill (1927a) and see letters Jokl to Hill, 1955-1976, AVHL 4/45.
[296] A.V. Hill (1931c); A.V. Hill (1932b); A.V. Hill (1933a); Crowther (ed.) (1933); A.V. Hill (1938); on the Physical Education Committee (Hill was chairman), see the files in FD 1/3982; and see letters Fletcher to Hill, AVHL II 4/27; files on air defence, in AVHL I 2/4.
[297] A.V. Hill (1933a): p.133.
[298] A.V. Hill (1935): p.356, and passim.
[299] A.V. Hill (1925): p.486; more generally, see Hoberman (1984); Berryman and R.J. Park (1992); Hoberman

Hill queried a 1933 audience (because 'Nothing perhaps can better illustrate nervous action than a short discussion of muscular skill'): 'What does a skilful muscular movement feel like to the performer himself; how does he control it as it proceeds; how does he learn it; how does he remember it; how does he reproduce it? [...] How is this done?'[300]

Unlike isolated organs, the athletic body offered a palpable, life-world model of energetic conversion phenomena; and as a scientific and cultural construct, as we shall see, it deeply informed Hill's expanding biophysical enterprise - not only the rhetoric Hill quite evidently indulged in, but its contents, perceived significance, even, its locale. As we shall see as well, it profoundly – and concretely – would shape the vision of nervous activity which would make its somewhat sudden appearance at the fringes of this body-minded enterprise.

Heat signs, 1926

The scene at the outset, meanwhile, barely seemed a physiological experiment. The equipment assembled here on this Easter Sunday indeed would easily have out-performed comparable out-fits at institutions such as the Physikalisch-Technische Reichsanstalt, Berlin, or the National Physical Laboratory in nearby Teddington.

But it was: on closer inspection, there was a little piece of frog's sciatic nerve somewhere amidst this jungle of cables, terminals, shunts, circuits, and resistances, carefully placed onto a custom-built thermopile, the latter itself artfully composed from several dozens of highly sensitive thermo-couples.

(1992).

300 A.V. Hill (1933c): pp.319-320.

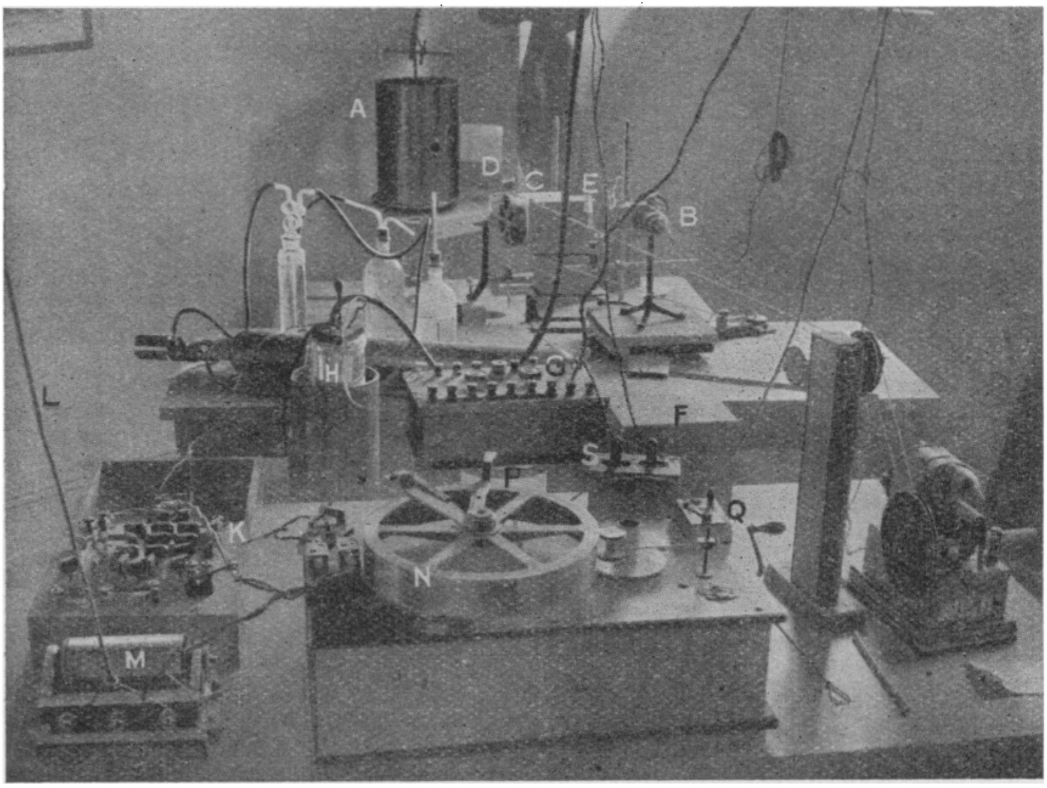

Figure 17: Hill's myothermic set-up, 1920

The aim was to determine the minuscule amount of heat the nerve liberates, or rather, should liberate, during the passage of a nerve impulse. In 1926, this was, amazingly, a far-from-settled question. For decades, physiologists had failed to detect any traces of energy being liberated by a nerve during its explosive activities. In 1848, even someone like Helmholtz failed – his instruments had a resolving power of 1/1000°C; Rolleston, a Cambridge physiologist, went down to 1/5000°C in 1890, still failing.[301] The 'propagated disturbance' is largely an 'intangible' entity, as Hill's somewhat senior collaborator Keith Lucas deplored in 1914, only a few months before this most promising physiological investigator fell victim to war, tragically dying in a plane-crash. The impulse's 'intensity', as Lucas ventured at the time, was 'untranslatable' 'into any physical or chemical meaning in the present state of our knowledge'.[302]

301 Lucas (1912): p.513; A.V. Hill (1912): p.433.
302 Lucas (1917): p.4; p.8; on Lucas, see H.H. Turner (1934).

In 1912, Hill himself had found – with a much more primitive electro-thermic implement than the one at his disposal fourteen years later - that for 'every single propagated disturbance the change of temperature ... cannot exceed about ... a hundred millionth of a degree'. These impressive numbers, widely received as definite, spelt the 'absence of temperature changes' during nervous conduction. The 'propagated nervous impulse', Hill's logical conclusion went, was 'not a wave of irreversible chemical breakdown, but a reversible change of a purely physical nature.'[303] Active nerve did not emit the signs of chemical, metabolic activity.

'Students', as Hill will have occasion to report still in 1929, in fact 'make experiments to show that it cannot be done.'[304] Laboratory manuals and text-books rarely failed to highlight this curious but brute fact: that although one had to 'suppose that nerve is living' it was 'impossible to suppose that any chemical process resulting in an irreversible loss of energy' was involved, or, for that matter, that nerve exhibited the certain, correlative phenomena: signs of *fatigue*.[305]

These signs of nervous activity, if they existed at all, were vanishingly small. And nerve thus seemed to behave very differently from muscle. This, as everyone knew from his or her own experience, was most easily fatigued indeed; this was a physiological object whose metabolic, dynamic, energetic nature was beyond doubt: elucidated to a degree no other physiological *machine* could match. Here, 'progress has depended upon the cooperation of many workers in many different countries', as Hill approvingly observed in 1932.[306]

But until around 1926, nerve resembled this machine not even remotely. And no biophysical instrument, to be sure, was fast and sensitive enough to keep up with the putative energetic signs emitted by nerve. The set-up at hand on Easter 1926, the result of

303 A.V. Hill (1912): p.440.
304 A.V. Hill (1929c): p.265.
305 So notably, for instance, the 'bible' of interwar physiology, Bayliss (1924): pp.378-379.
306 A.V. Hill (1932c): p.62.

more than a decade of patient tinkering, tweaking and experimenting with muscle, was able to resolve heat production to just about less than 0.000001° C.[307] Staggering numbers: this presented the very limit of what could be measured in those days. Were one to go any further, as Hill alerted in that very same year in the Journal of Scientific Instruments, random molecular fluctuations began to haunt the galvanometers.[308]

Hill, however, mastered his subject. After the Great War, it was William Hartree, a Cambridge mechanical engineer and someone excelling in the art of algorithmic, and thus *objective* records-analysis, who had helped Hill to perfect the technique. By 1932, 'absolute limit[s]' would be reached in this connection.[309] After the war, Hill also had hired Downing, his personal mechanic, 'an artist in the finer details of instruments manufacture' as Hill often praised him, and 'practicably irreplaceable'.[310]

In 1926, one was, accordingly, able to operate the 'most refined apparatus available.'[311] These were reasons for being optimistic. Yet, even so, this nervous heat would be no more than an accumulative effect, to be obtained after several minutes – 'prolonged bouts' - of intensely stimulating the little nerve with high-frequency currents. And there were a myriad other uncertainties. In the morning of Easter Sunday 1926 several hours thus already had passed so as to ensure uniform temperature distribution through-out the set-up. It clearly was a precarious, and utterly invasive high-precision manoeuvre, permanently threatened not only by random molecular fluctuations, but, as Hill worried, by the imprecise non-uniformity and 'the possible deterioration of the nerves' as well.[312]

The basic procedure, meanwhile, was the exact-same as with muscle. Any heat liberated by this living nerve, if indeed, there was any heat liberated, would induce an electromotive force in the thermopile; this force, in turn, would be measured by the

307 A.V. Hill and Hartree (1920): p.110.
308 A.V. Hill (1926c); A.V. Hill (1913): pp.30-31.
309 A.V. Hill and Hartree (1920): pp.100-106; Hartree and A.V. Hill (1921); A.V. Hill (1932d): pp.111-112.
310 Hill, 'Application to the Medical Research Council', 27 September 1933, FD 1/1949
311 A.V. Hill (1926a): 163.
312 Downing, Gerard, and A.V. Hill (1926): p.233.

galvanometer connected to the thermopile, the effect propagated, amplified and hopefully made perceptible through still more galvanometers one had mobilized for this special occasion. They were coupled via photocells: a *thermo-relay*.

As important here - as one would be dealing with incredibly more subtle phenomena - was that everything be recorded 'photographically' so as to accurately register the output-galvanometer's transient, barely visible deflections.[313] The photographic records in due course would have to be subjected to the painstaking analysis which one had developed to make sense of the muscle records – a mix of mechanic, algorithmic procedure and, it had to be acknowledged, somewhat arbitrary guesswork. This step too was essential: it was necessary to dissolve the compound effect – what actually could be measured - into its putative series of causes: the instantaneous heat liberation at any given moment.[314] This was, as Hill and Hartee explained it, a problem familiar from other domains where 'curves represent[ed] sound waves, tides or other periodic vibrations': The kind of records analysis required was very similar to the 'resolving [of] a tide or a sound wave into its several sine-curves. '[315] Both Hill and Hartree indeed had ample experience with the latter – during the war, they had spent a great deal of their time on devising sound locators for the purposes of anti-aircraft defence.[316]

The way it was framed here, nerve – replacing the muscle in the system - thus presented not least a formidable technical problem: only more difficult. The result of the above analysis, meanwhile, looked familiar. To Hill and his little team the diagram they produced must have seemed deeply reminiscent of physiological, muscular activity. The impulse here was inscribed not as a sweeping curve – its familiar appearance. Rather, like muscle, nervous action here decomposed into a sequence of events or distinct 'phases'.

313 A.V. Hill and Hartree (1920): p.115.
314 Ibid., pp.100-106.
315 Ibid., p.101.
316 A.V. Hill (1924b); and see Pattison (1983); Barrow-Green (2007).

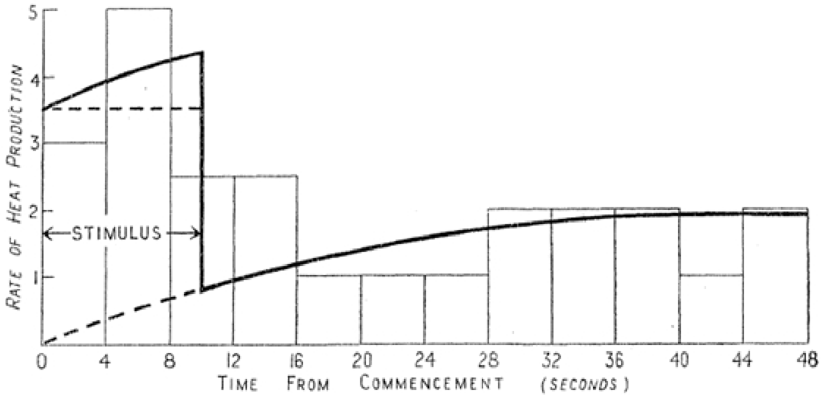

Figure 18: Nerve heat, 1926

The energetic vision of process that had become embodied in these bar-charts - the product of thermometric curve analysis - had resurfaced underneath the nerve impulse: the 'time relations' of the *events* underlying the nervous conduction process. Thus, in visible analogy to muscle, there were clearly discernible here an 'initial heat' phase of apparently explosive heat production; it was followed by a 'delayed' phase of heat liberation which was possibly associated, in turn, with a process of 'recovery'.[317]

These were the first and compelling signs of what was quite evidently, as Hill perceptively noted, something of an 'analogy of muscle'.[318] It was not a perfect one. Frog nerve, the three London biophysicists diagnosed quickly, notably did not exhibit 'the sharp division into an initial heat, intense but brief, and a recovery heat, small but prolonged, that is typical of muscle.' Indeed, though the fact of nervous heat liberation was established beyond doubt, in these nerve-experiments the ratio of the 'initial' and 'recovery' heat-phases differed suspiciously from the ratios one had observed in muscle. In nerve, it was especially the delayed phase that prominently appeared in the records. In fact, the characteristics of these phases seemed different enough, Hill concluded, so as to 'prohibit any possibility' that the exact-same chemical machinery was involved.[319]

317 Downing, Gerard, and A.V. Hill (1926): pp.245-247.
318 A.V. Hill (1926a): p.164.
319 Ibid.

But there was resemblance enough. Hill and his muscle-experienced co-workers, in turn, would lose no time to latch on exactly this seemingly analogous behaviour of nerve. Still in the course of 1926 they consequently began mobilizing the entire arsenal of manipulative practices and experimental protocols that had been devised in connection with the myothermic technique so as to hopefully give more definition to these putatively distinct 'phases': this meant trying to separate, enhance, and modulate the elements of the sequence of events that their records had begun to uncover. Quite successfully so, nerve here was treated like a muscle – and, as we shall see, crafted even more definitely into one.

As with muscle, for instance, poisoning the nerve with veratrine or iodocetate, it so turned out, enhanced recovery heat production up to 1000%;[320] varying the temperature of the preparations had similarly striking effects in both cases, and on the character of the initial heat in particular: if the instruments could not be made 'quicker', as Hill explained the reasoning behind this particular manoeuvre, 'the only possibility was to make the nerves slower, viz., by cooling to 0° C.'[321] Or again, by way of suppressing the nerve's aerobic activity by immersion of the tissue in nitrogen, one should be able, as Gerard said, to similarly 'cut out' certain elements of the sequence of phases.[322]

On the level of interventions, the analogy between muscle and nerve was palpable. In this well-insulated London basement laboratory, the model-function muscular activity quite suddenly had assumed was about *doing* things rather than *words*, and *intervening* rather than *representing*. Crafting nerve as a muscular-like phenomenon was a matter of analogy made concrete: of transfer – of techniques, experimental interventions, diagrammatic representations. Already their feat of Easter Sunday 1926 was nothing but the result of a rather 'bold' transfer, as Gerard noted, of an entire experimental system - from muscle to

[320] Feng (1932); Fromherz and A.V. Hill (1933).
[321] A.V. Hill (1932d): p.142.
[322] Gerard (1927a); Gerard (1927b).

the much more delicate object nerve.[323] And some sense could be made of these observations, accordingly, 'if one 'imagine[d], on the analogy of muscle contracting anaerobically' that the initial outburst of heat perhaps was similarly associated with a chemical process such as lactic acid formation.[324]

Even so, the picture one was able to form in 1926 of this heat liberation was still very crude. Or rather, it was utterly precarious and non-transparent. The intensity of liberation, though hovering disturbingly close to the limits of the measurable, seemed significant enough to now make plausible – in analogy to muscle - the presence of some energy-consuming chemical *change* underlying the impulse: the explosive event as such. But whether or not this involved a process similar to lactic acid formation was unclear; and even the very presence of a chemical change was, as Hill cautioned, a far from necessary inference. So excessively small seemed the *initial heat* in particular that the impulse perhaps was of a purely physical nature after all. A mere ionic 'mixing' process such as would follow the breakdown of the nerve membrane, for instance, was still perfectly conceivable as an alternative account. Clearly, the 'investigation [was] not complete', as Hill submitted.[325]

More disturbingly even, there was no immediacy in this practice, no complete eradication of subjectivity, no *direct* knowledge to be gained of the individual impulse. The heat 'per impulse' was a calculated event: a product of numerical analysis.[326] Worse: these heat liberations were, as we have seen, cellular behaviours provoked by way of problematically invasive procedures: by subjecting nervous tissue for many minutes to extreme 'exhaustion' and 'fatigue', by immersion into nitrogen, and by cooling nerve to unphysiologically low temperatures. None of this rendered the phenomenon any less

[323] Gerard (1927a): p.352.
[324] A.V. Hill (1926a): p.164.
[325] Ibid., p.163; p.165.
[326] Crudely, this meant, first, to estimate the 'total' initial heat production, and second, to gauge the heat-per-impulse by dividing this compound effect – the result of several minutes of electric stimulation - by the estimated total number of impulses. The latter, meanwhile, or so one could assume, was roughly proportional to the frequency of the stimulation current.

precarious in the eyes of the physiological community at large, where one quickly took note of these new horizons. Could indeed anything be inferred about 'natural excitation', in the words of one especially worried observer, under such extreme living-conditions and on the basis of such massive 'artificial interventions into the processes of life'?[327]

Natural exhaustions

So looked the frontiers of investigations into in the fundamental nature of the nerve impulse in about 1926. It was 'obviously impossible to assess', the *Lancet* noted, just what the benefits for medicine might be. 'Its direct value is probably nil'.[328] The impulse's exact fundamental nature, on the other hand, whether it was a purely physical event or perhaps more of a chemical reaction, its time-course or the character of the ominous *alteration* the cell's delicate surface film presumably underwent during the passage of an impulse – all these difficult questions would essentially depend on the amount of heat liberated per impulse.

Or we should say, so these frontiers appear as seen from Hill's biophysical basement laboratory. Seen from there, it was a matter evidently of only a few months that the 'heat production of nerve' transmuted from a non-entity into a scientific phenomenon. And seen as a technical problem, this, in essence, was the *analogy* that was being forged between muscular and nervous activity. Not much more would need to be said about this analogy, or the model-function of muscular activity, if this transfer had not taken place - and would not take further shape - in circumstances which not only supplemented it as a *practical analogy*, but turned it into much more than a technical affair. Like the physiology of isolated muscle itself, the transmutation of nerve heat liberation from something

327 Winterstein (1929): p.16.
328 nn. (1926b).

excessively small, opaque and dubiously artificial into a natural and genuinely physiological phenomenon was mediated – both scientifically and culturally – by a world of muscular activity and bodily movements. Neither its fundamental importance alone nor its difficulty as a technical problem explain the significant re-conceptualizations of nervous activity that were in the process of being crafted: the shift away, that is, from the predominately 'physical' conceptualizations of nervous excitation, and towards detailed considerations of energetic processes and underlying mechanisms.

As we shall see in the remainder of this chapter, much more was required so that nervous excitation transformed from an essentially muscle-unlike phenomenon into more transparent and natural object whose process-nature was - essentially, practically, conceptually – analogous to muscle. This is the significance of the broader historical circumstances to the case at hand: the sciences of muscular activity, both 'fundamental' and in its 'applications to man', had prepared, were shaping, and would envelop the emerging picture of nervous activity in almost any respect. To see this, we indeed have to adopt a different, less intuitive vision of what was encompassed in the interwar sciences of nervous activity. These centred not on brains, not even simply on nerve messages, but crucially, like Hill's own enterprise, on bodies and muscular skill.[329]

Hill was eager indeed when it came to committing his own environs to the study of 'human (or applied) physiology' - as had first happened some six years before he returned to nerve, at Manchester. Hardly arrived, Hill then promptly enrolled several of his new colleagues who were, he judged, very well suited for such a venture:[330] Bryan McSwiney, the lecturer in experimental physiology, had been conducting work for the IFRB already; F.W. Lamb, at the time pioneering a 'human experimental physiology' in Manchester, harboured similar interests (later, for instance, diverting Royal Air Force tests for the 'assessment of

[329] On this quasi-obsession with the peripheral nervous system, see esp. J.Z. Young (1951): p.8; pp.40-41; Walter (1953a): pp.27-28; Gerard (1958): p.199; p.233; Zangwill (1964); Braslow (1997); R. Smith (2001b); Hogenhuis (2009).

[330] See esp. letters Hill to Fletcher, 17 July 1920, Hill to Fletcher, 21 September 1921, FD 1/3764

schoolboys'); and there was physicist-turned-industrial-psychologist Tom Pear of the Experimental Psychology Department which, conveniently, was located in the same building.[331] The general objective, Hill told Fletcher, would be to 'measure, define and study the normal functional activities of man'.[332]

But rather than invading the factories to unravel the physiological basis of industrial living, Hill and his assistants, first in Manchester, and from 1924, in London - 'healthy young men' and 'vigorous male subjects' - preferably exhausted themselves when it came to applying biophysical knowledge to man. In Hill's own, programmatic words this meant 'press[ing] to its logical conclusion the physico-chemical view of muscular contraction arrived at by the investigation of the isolated muscle'.[333]

Easily the most significant such allegedly logical conclusion concerned the so-called *oxygen debt* that the athlete, soldier, and factory labourer 'incurred', it turned out, as each went about his after all not-so-very-different business – at hopefully 'optimal speed' and 'optimal performance'. The concept of oxygen debt, promulgated by American aviation physiologists and German hygienists alike, would make a grandiose career in the interwar physiology of work.[334] It will be of some importance here as well: a palpable matter of extreme exhaustion and fatigue, it eventually would make a fundamental but genuinely physiological come-back in connection with the nerve impulse.

It was Hill himself who had first introduced the concept, along with a corresponding measurement technique during his Manchester period. Both, concept and technique, were strategically geared towards the 'modern', *anaerobic,* theory of muscular contraction. Constructed as an indirect measure of lactic acid concentration, 'oxygen debt' brought home, in the words of Hill's Japanese assistant Furusawa, how the aggregate activity of 'nearly' all the muscles in the body together 'resemble[d] ... exercise in the

[331] See Lamb (1930); on McSwiney, see G.L. Brown (1948); on Pear, Costall (2001).
[332] Hill to Fletcher, 17 July 1920, FD 1/3764
[333] A.V. Hill, Long, and Lupton (1924a): p.334; A.V. Hill, Long, and Lupton (1924b): p.138
[334] E.g. 'Department of Applied Physiology, Draft for Annual Report', 1923, FD 1/1215; Campbell (1924); Steinhaus (1933): pp.128-129; Atzler (1938): pp.348-352.

isolated muscle.'[335] In the ideal case of 'the more athletic human subject, in fair training' athlete and isolated muscle almost became one. Spelt out in these athletic registers, muscle and man converged in extreme performance: these processes then approximated, Hill ventured, '*a degree of exhaustion not far short of that attained in direct artificial stimulation of the isolated muscle.'*[336]

The essential idea behind such *debt* was simple and sportive: the more severe the exercise, the more intense lactic acid production, the less oxygen supply during exercise will keep up with removing it, the more lactic acid will accumulate: the greater would be the oxygen debt at the end of the exercise, that was, the oxygen consumption required to 'restore' the athlete. Moreover, unlike lactic acid concentrations, oxygen debt, defined as the excess oxygen consumption *after* exercise, was fairly easily determined by adapting standard techniques that had long been in use for purposes of respiration measurements (such as, notably, the so-called Douglas bag). As Hill argued, this

> capacity of the muscles for incurring very large oxygen debts is fundamental to their function in the body. ... It is clearly necessary for the body to have a store of energy of some kinds available, which can be liberated at a high rate when required, to be restored later by the slower processes of oxidation.[337]

And in these regards, almost everything, it soon emerged, was a matter of bodily *skills*: of exactly how this debt, or its correlate, a 'store' of energy, would be managed. Bodily efficiency, it soon was amply confirmed, was principally a matter of training, improved practice, and 'better [neuromuscular] coordination'.[338] As one IFRB report worded it in a telling turn of phrase, at Hill's *Biophysics Unit* scientists were penetrating deeply into the all-important problem of the 'economy ("skill")' with which bodily energies were in fact expended.[339]

335 Furusawa (1926): p.155.
336 Hill, Long, and Lupton (1924b): p.134.
337 Ibid., pp.134-135.
338 Steinhaus (1933); Dill and Bock (1931): pp.1-3.
339 HMSO (1927): p.15.

Though framed as a matter of identity, logical conclusions and application, the athlete-as-experimental-object was, from the perspective of isolated muscle (and nerve) all about added complexity. Far from being reduced to an isolated organ, the athlete supplemented the activity of muscles with a physiological affluence that hardly could have been gleaned from a piece of frog muscle soaked in Ringer solution: not merely fatigue, but energetic stores, debt, skills, optimal performance, efficiency and, as we shall see shortly, much more – at issue was the *genuinely* physiological, *natural* significance of the anaerobic nature of muscular activity.

Funded by the MRC, the considerable body of work Hill would devote to pressing these logical conclusions forward appeared under the heading 'Principles Governing Muscular Exercise' in the reports of its Industrial Fatigue Research Board. Throughout the 1920s and beyond, while advancing the natural knowledge which there was to be had of isolated organs and of the subtle phenomena they displayed, Hill and in total some 10 collaborators busied themselves cementing the in-principle identity of isolated muscle and the whole man. Experimenting on themselves, laboratory inhabitants, outdoors or on bicycle ergo-meters, on local sports clubs, university students, wooden athlete dummies in wind tunnels or Olympic athletes, Hill and allies investigated the characteristics of energy expenditure and recovery processes in moderate and severe forms of exercise, uncovering, along the way, the efficiency of single movements in relation to speed-of-motion, the air-resistance of a sprint runner, and most notably so, of course, its dependency on the 'economy ("skill")' with which the available energy was used.

Many 'industrial processes conform[ed]', as one IFRB report noted, to exercises and bodily movements of this more leisurely kind.[340] And more significant even for present purposes, despite the rhetoric, such conforming was not merely about the 'application' of

[340] Ibid.

physiological science. The athlete in particular began to generate knowledge as much as it rendered existing knowledge unproblematic. It was here exhaustion turned natural, familiar and truly physiological.

With his sometime colleague Pear in particular Hill thus felt in deep agreement that 'the word "fatigue"' would have to fill one with 'ennui and biliousness'.[341] Fatigue was too simplistic a vision of man's functionalities as Pear masterfully outlined in tracts such on 'The Intellectual Respectability of Muscular Skill' and similar writings.[342] Like Hill, Pear had found in the dexterous athlete a model scientific object. The rapid movements of the athlete now finally would yield to some 'higher form of thought analysis', Pear enthused, thanks, among other things, to ultra-rapid cinematography, diagrams and also, the special symbolic notation systems Pear was busy devising.[343] The problem, the techniques, the very object – here everything was a most appropriate sign of these modern times.

Carrying such ideas into factories and sporting grounds alike, Pear himself was grappling with the incommunicability of tacit knowledge avant-la-lettre, especially, the difficult but quite obviously important problem of acquiring muscular skill (which at present, he said, 'possessed no usable language').[344] Pear's *Skill in Work and Play* (1924) nonetheless managed to address a great many people, also conveying something of the tremendous conflation of social boundaries - of athletic life and industrial existence - interwar students of muscular motion very casually advanced: scientists, industrialists (who may 'skip the illustrations taken from games'), and 'open-air athletes' (who may 'avoid ... those paragraphs containing the word industry') all equally belonged to the target audience.[345] Meanwhile, Hill himself had been turning the phenomena accompanying such skilled, vigorous movements into a persuasive test-case for the fundamental principles of muscular action.

[341] Pear to Hill, 13 January 1925, AVHL II 4/67 ; Hill to Fletcher, 1 June 1931, AVHL II 4/27
[342] Esp. Pear (1924); Pear (1928).
[343] Pear (1924): p.44; p.76; nn. (1925b): p.7; nn. (1925a): p.22.
[344] Pear (1924): esp.pp.19-20; pp.24-25.
[345] Pear (1924): pp.10-11; on this conflation, see esp. J.J. Matthews (1990).

In this connection, the advent of the anaerobic view of muscular contraction had seriously disqualified earlier attempts to determine the energetic expenditure of the working man. Simplistic determinations of oxygen consumption, as Hill pointed it out in 1924, were now facing severe limitations. The newly *anaerobic* nature of muscular activity undermined the very idea; fluctuations in oxygen consumption additionally disqualified oxygen consumption as a reliable guide to energy expenditure. And these, of course, were especially in the evidence when in came to complex, athletic manoeuvres and very brief and 'very violent' forms of exercise.[346]

The delicate functioning of this athletic body depended, as Hill's many experiments showed, 'not chiefly on power but on skill and rapid co-ordination'.[347] Unlike the labourer bent over assembly lines and machine tools, unlike the isolated organ in its artificially composed, electrolytic bathing fluid, the athlete arguably manifested physiological activity in all its authentic, unalienated richness.[348] Maximum bodily efficiency could only be achieved, one was accordingly advised, if the body be 'co-ordinated and integrated into a harmonious whole'. This kind of integration, as everyone knew, was displayed to perfection in the (ideally) 'metronome' -like hurdler or 'the gracefulness of the expert dancer or figure skater'.[349]

346 A.V. Hill (1924a): pp.511-512.
347 A.V. Hill (1935): p.24.
348 E.g. A.V. Hill (1927a); Lowe and Porritt (1929): p.224; Dill and Bock (1931): pp.1-3.
349 Dill and Bock (1931): pp.1-3; Lowe and Porritt (1929): p.226.

It will thus be seen that the process of crossing a hurdle is an intricate one, and before that essential

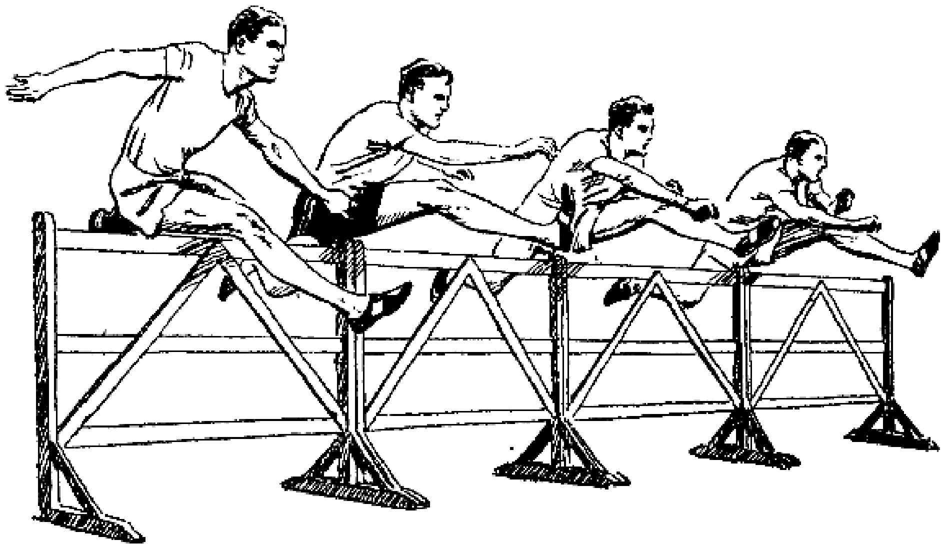

FIG. 9.

accuracy can be obtained which permits of perfect equilibrium and control being maintained during the flight and at the same time an efficient conservation of energy, much consistent, intelligent and painstaking practice will be required. Hurdling does, in some respects, conform to a type of field event in that the optimum is reached only by a complete mechanisation of the action. But, assuredly, the confidence gained by an increasing proficiency in style is a sufficiently valuable asset to the hurdler to be worth much seeking.

Figure 19: 'complete mechanisation of the action', 1929

Athletic performance was not only about surplus physiological complexity. It was that, but as an *approximation* of the isolated organ, it also functioned as a model-case of physiological authenticity. Not least in Hill's own numerous writings on the subject the athlete was put to use effectively, radiating its authentic naturalness and familiarity. To 'fatigue a frog's gastrocnemius', as Hill thus at times conceded, 'may seem - does seem to many - an irrelevant pursuit'. 'It is different however', Hill would continue, 'if we realise that almost exactly the same results occur in us if we run upstairs too fast.[350] *Muscular Movement in Man* (1927), Hill's first-ever monograph did not dwell much on the question 'Why investigate athletics, why not study the processes of industry or of disease?'[351]

Here was beauty and strength, and being in 'state of health and dynamic equilibrium', athletes could 'repeat their performances exactly again and again'. There was more to such deferring than met the eye: if excessive, artificial interventions into the normal operations of living, isolated organs was methodologically utterly problematic – the very act of isolating them, subjugating them to prolonged, repetitive stimulation, and the resulting exhaustion and extreme fatigue – the athlete's exhaustion and extreme fatigue was beyond such nagging suspicions. At least of recent: this positive valuation of extremes, records, and professionalism in sportive behaviour itself was a recent development.[352] The strenuousness endured by the athlete surely was 'a sufficient commentary' [sic], as Hill silenced his critics, to the idea that the 'performance' of isolated muscle would be 'abnormal': 'The muscles of a subject who can walk 9 miles without obvious signs of fatigue are no so "abnormal" that a physiologist need despair of investigating them.'[353]

Far-from-equilibrium

The athlete was the paradigmatic vital, energetic phenomenon. It was this phenomenon not merely in the form of abstract, biochemical balance-sheets and isolated organs soaked in electrolytes. Physiologically, the athlete stood for phenomenological familiarity and genuine nature. Fabricated as such a natural thing, it was far from incidental to Hill's biophysical mission. By the early 1930s, the 'cognizance of the oxygen debt' had resulted in an

[350] See Hill, foreword to Lamb (1930).
[351] A.V. Hill (1927a); cited in Bassett (2002): p.1573.
[352] Guttmann (1978); Holt (1990): chapter 4.
[353] A.V. Hill and Kupalov (1929): pp.320-321.

impressive range of studies. Debts were incurred anywhere from runners to movers of wheel barrows to pilots exposed to low barometric pressure.[354] In the process, the fundamental action of tissues as well - laboratory effects resulting from artificial interventions, that is, which were not easily fathomed either in their finer details nor in their general, physiological significance - were turning into more palpable phenomena, natural, energetic, cyclic: intimately familiar to all.

Delivered in 1926, Hill's Croonian lectures on the *Laws of Muscular Motion*, first boasted the anaerobic 'change' followed by oxidative recovery as a 'well-nigh universal' cycle. This 'common principle', nothing else of course than the lactic acid mechanism, manifested itself, much recent evidence suggested, in 'the cross-striated muscles of man, frog, and tortoise as in the smooth, slowly reacting muscles of marine invertebrates' alike.[355] It was, consequently, 'natural to regard oxygen-want, as such,' as Hill reinforced the message a few years later, 'as the agency provoking degenerative change.'[356]

Oxygen debt, energetic stores, cyclic, energy-consuming processes here suddenly reappeared on the fundamental level of tissues. The subject of skilled performance and the economic uses of energy – athletics - had indeed brought home something almost unheard of when it came to isolated organs, as we shall see now. It was the *oxygen debt* itself, and its mirror phenomenon, an energetic *store*.[357] More peculiar even, it was the condition of a 'steady state oxygen debt' that imposed itself on these British biophysical investigators - the correlate of a 'steady state' of exercise. Such a state was gradually setting in – provided exercise was gentle enough - at 'optimum speed': 'optimum performance'. For in such a case, lactic acid formation exactly balanced its oxidative removal, the 'contemporary supply' of oxygen, meanwhile, replenishing the energetic store. It was a peculiar, active and

354 Steinhaus (1933).

355 A.V. Hill (1926d): pp.88-91.

356 A.V. Hill (1928b): p.160.

357 The idea of energetic stores in tissues, to be sure, wasn't entirely new. Notions such as oxidative molecules, biogen molecules and similar concepts were widely floated in the late nineteenth century, but had become thoroughly disqualified since as being vague and smacking of mysticism. See esp. Bayliss (1924): p.18; Gerard (1927c): p.401; and on the so-called 'alteration' theory, Lenoir (1986).

dynamic condition: far-from-equilibrium.[358]

By 1930, what had begun as an athletic *condition* was transmuting into a fundamental principle of life. As Hill's *Adventures in Biophysics* lectures (1930) had it, the living state had everything to do with a 'continual liberation of energy' that made the living cell 'evade' the attainment of true equilibrium state; and it had everything to do, therefore, with certain 'delicate governors' of energy as well, rather than, as Hill surmised, with peculiar *Lebenswirkungen*.[359] The energetics of the impulse and muscular contraction, so much was suggested by the *analogy of muscle*, were fundamentally alike. The 'whole business' had 'an exact counterpart of what happen[ed] in a long-distance runner, walker or a bicyclist'. Activity, exhaustion, recovery, regulation - the 'problem', Hill trumpeted it out by 1930, was 'in a sense, a single one in all these cases'.[360] The nerve impulse, muscular performance, the long-distance runner, as Hill laid it out here, they all revealed just how far the living cell departed from merely being an energetically *passive* system.

Activity was about 'active living cells': a 'dynamic steady state'. In all these convergent cases, there was energy liberated, actively, continually, somewhat mysteriously, which maintained life in a state far from equilibrium. 'How that energy [was] supplied' had now become, Hill declared, 'the major problem of biophysics.'[361]

Historians of biology are familiar, of course, with the much broader transformation at issue here. Hill spearheaded this transformation along with a number of more familiar names, notably Walter Cannon, L.J. Henderson, August Krogh, and Joseph Barcroft: homeostasis, the *wisdom of the body*, physiological regulation, buffer systems, dynamic equilibria, fixity of the internal environment were the ideas they and a great many others brought 'up-to-date', in Barcroft's words, during those years.[362] Indeed we tend to

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358 Esp. A.V. Hill, Long, and Lupton (1924b); also see A.V. Hill and Lupton (1922).
359 A.V. Hill (1931a): esp. preface; pp.55-60; pp.77-79; also see A.V. Hill (1930).
360 A.V. Hill (1931a): p.73; pp.77-79.
361 A.V. Hill (1931a).
362 Quoted is Barcroft (1934): p.1; also see Cannon (1929); Henderson (1928); Krogh (1939); more generally, on Barcroft see Franklin (1953); F.L. Holmes (1969); on Cannon, Wolfe, Barger, and Benison (2000); on Henderson, see Hankins (1999); Chapman (1990); on Krogh, see A.V. Hill (1950).

know of these developments as matters of theory, ideas, and intellectual influence rather than as histories of practical physiologies.[363] But these essentially convergent visions we need to imagine as being profoundly shaped by the practical, not intellectual, body-centred problems of the interwar years. Like Hill himself, even this prestigious cast of academics all were deeply enmeshed in the physiological practicalities of modern living: Henderson then steered the Harvard fatigue laboratory; in Copenhagen, the 'zoophysiologist' Krogh commanded a little empire not unlike Hill's - besides animal physiology, his laboratories housed medical physiology, biophysics, and an Institute for the *Theory of Gymnastics*; Barcroft, a Quaker and also a Cambridge man, was an acclaimed authority on nerve gases, and many times had pushed his personal respiratory limits on high-altitude expeditions that took him and his Cambridge assistants to far-away, and extreme places (this was, no doubt, an all-round exacting and sportive science: it required, as Henderson approvingly noted, 'literary art to bring out the sporting aspects of oxy-haemoglobin curves');[364] and so for Cannon's *homeostasis*: his take on the matter owed a very great deal to the countless observations by himself and others on the physiology of fear and flight and fight reactions during war (soldiers) and peace (cats).[365]

These were the crystallizations of fundamentally the same, concrete problematic. Expose a man (or a woman) to any extreme environment - severe exercise, high altitude, the factory, the trenches – and so many homoeostatic mechanisms will ensure that the fixity of the internal environments will remain 'remarkably constant' - provided a continual supply of energy.[366]

It was not long until Hill had recognized such dynamic *steady states* during his pioneering experiments on runners. But back then, in the early 1920s, nothing comparable was known to, or had much interested, the students of isolated organs. This is hardly

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[363] See especially, S.J. Cross and Albury (1987); also see A. Young (1998); related, also see Fox-Keller (2008).
[364] Henderson (1926), quoted in Franklin (1953): p.160.
[365] on the latter (cats), see esp. Dror (1999); and Harrington (2008) chapters 2-3.
[366] Barcroft (1934): pp.1-4.

surprising because there the energy-consuming phenomena that might have accompanied the continual, vigorous *performance* of an isolated organ were far from salient: any hint of extreme exhaustion was, as we have seen, in fact deeply suspicious. *Exhaustion* always was dangerously coming close to the *destruction* – by 'electrocution' - of the tissue.[367] And quite simply, one was lacking the means, or in any case, the rigorous means, to say much concrete about the dynamics of intra-cellular, biochemical processes, anaerobic, oxidative or otherwise.[368]

And thus, the crucial *mediating* role which the analogy of muscle - *enlivened* by the athlete – assumed: It made palpably real the concept of a dynamic, non-equilibrium state. Oxygen debt by any criterion was a matter of precision. And as such - its *indirectness* as a measure notwithstanding – it considerably altered the position as to how the dynamics of physiological energy conversion were to be, or could be, conceptualized.[369] By 1930, Hill would query the audience of his *Adventures* lectures above (rather ominously, and in italics): '*if there be no equilibrium, how far dare we apply the rules and formulae derived from the idea of equilibrium*?'[370]

The idea that had become very questionable indeed, Hill thought, was that of a *passive*, thermodynamic equilibrium, and thus, the great many rules and formulae of physical chemistry that by the time pervaded, of course, physiological science rather generally.[371] But Hill's was no romantic backlash against these essential tools of physiological rigour.[372] Rather, as we shall see in detail now, in between the performances

367 E.g. A.V. Hill and Hartree (1920): pp.106-107; Meyerhof and Lohmann (1925): p.793; A.V. Hill (1928b): pp.150-151 .

368 To be sure, this situation was subject to change at a rapid pace in the 1920s. Biochemists in particular began to eludiate cell respiration, Atmungsfermente and the like; such advances didn't necessarily however much advance the puzzles of physiological function. Most familiar, the biochemical dimensions of the subject are associated notably with names such as Warburg and Keilin, see e.g. A.V. Hill (1928a): esp. p.159; Krebs (1972): pp.641-647; Slater (2003); Nickelsen (2009): pp.82-83.

369 On this, see esp.Agutter, Malone, and Wheatley (2000); Fox-Keller (2008).

370 A.V. Hill (1931a): p.160.

371 Some typical literature in this connection includes, Bayliss (1924); Steel (1928); Michaelis and Rona (1930); Wishart (1931); on a more theoretical note, see e.g. Donnan (1927).

372 The equation of holism and some romantic anti-positivism is, of course, quite widespread, see e.g.Harrington (1999); on the limitations of such views, see esp.Mendelsohn (1998); also see Anker (2002).

of isolated organs and the whole man, Hill had finally begun to discern a great principle at work: the 'very fundamental role of oxidation in maintaining the dynamic equilibrium' of excitable tissues.[373]

If the fundamental physiology of isolated muscle had yielded a picture of a sequence of microscopic events, the athletic subject added *performance*: a vivid, exacting picture of process and energy - its conversions, restoration, exhaustion, storage, its modulations, and optimal and economical utilisation. The athlete, that is, saturated the fundamental phenomena of heat with natural, real significance and translated them into genuine, physiological meaning. There was not an inkling of holism and vagueness in this science of exercise. Oxygen debt was palpable, the heat liberated by muscle (not to mention nerve) was not.

Returning now to this dynamic, energetic vision of the impulse will reveal how deeply the science of muscular exercise had pre-structured the cognitive space wherein which the heat production of nerve would take its place. Despite Hill's mastery of precision instrumentation, and despite the analogy of muscle, this was, we will remember, still far from secure. Even setting its several critics aside, if anything, progress threatened to undermine again the heat sign of the nerve impulse as a genuine, natural event.[374] Especially the small but noticeable improvements in instrumentation that had been achieved since 1926 - improvements in galvanometer speed and thermopiles - had the 'curious' consequence of progressively diminishing estimates for the 'initial heat'. The more rapid galvanometers brought estimates down from 11% to 9% of the total heat production; by 1931 the initial heat even dwindled to only 2%.[375] Could it be, so Hill was again prepared to ask, that further improvements would 'reduce the initial heat to a still

[373] A.V. Hill (1928b): pp.159-160.
[374] See esp. Winterstein (1931); Winterstein (1933); and see Amberson (1930).
[375] E.g. A.V. Hill (1929a): esp. p.173.

smaller fraction, or perhaps nothing it all?' A disturbing thought: after all, the absence or presence of the *initial heat* component especially was 'of fundamental importance in discussing the nature of the nervous impulse' - the *explosive* change: chemical process, that was, or a purely physical one? A physiological reality, or an artefact of intervention, measurement and analysis?[376]

True nature, authenticity, vigorous performance

If the fabrications of the athlete took shape as the natural, complex, and phenomenologically familiar counterpart to the precarious, artificially induced performances of isolated organs, the athlete-as-object was not the only such site where natural authenticity and biophysical science crucially came together. Indeed, much more could be said here about these configurations of the natural and the artificial. In Hill's experimental life, and in the sort of biophysical science that he fostered among his disciples, the athletic was always and everywhere exerting its influence. The public image that Hill fashioned for himself (and his body) at the time - an exemplar of the healthy man, physically and deliberately subverting the stereotypical image of the other-worldly, inhuman, ethereal professor - would be an example itself. As newspapers would typically portray him, the 'convention of a dry-as-dust professor was never shattered more completely than by Prof. Hill' (who 'seemed almost the last man in the world to spend laborious days in the laboratory').[377] As much as the skilled, athletic body helped to render the physiology of isolated organs authentic, Hill's own looks, his 'great vigour and freshness', ran distinctively foul with the widely alleged *distance* of science to the daily life and its artificial, inhumane character as well.[378]

[376] A.V. Hill (1932d): p.110; also see Bronk (1931).
[377] This particular example comes from the Daily Express (1928), quoted in Hill, Trails and Trials in Physiology, op.cit. pp.151-152
[378] Ibid.; on the prevailing mood, see Mayer (2000); more generally, see Overy (2009); and on stereotypes of

Hill's own *Chemical Wave Transmission in Nerve* (1932) even went further, venturing how 'our bodily habits affect even our theories of the nature of things'. It was something well illustrated, Hill mused, by 'the influence of ball games on doctrines of the constitution of matter proposed by British physicists'. Biological science, accordingly, was the most 'fundamental science' of them all because the behaviour of the nervous system was 'the ultimate basis of all intellectual activity.'[379] And for the likes of Hill (quite apart from the evidently polemic nature of these remarks), this ultimate basis, as we can begin to see, did not spell *central* nervous system. It was a fundamentally embodied and embedded affair: bodily skills, habits, and graceful *neuro*-muscular coordination stretching out all to the peripheries.

Invoking Hill's own athletic physique is indeed not only an aside.[380] In parallel to the first signs of the heat production in nerve, there was established among Hill's biophysical circles new bodily habits, and with them, appeared a new scientific locale - and a new experimental object. As this section shows, this development crucially complemented the employments of the athlete. They all conspired and propelled the *initial heat* – that event supposedly associated with the explosive reaction of nerve, the impulse – more comfortably into the domain of the authentic, dynamic, and genuinely physiological. In terms of its cultural complexity, there was more to the model-function of muscular activity than merely muscle, the athlete-as-object, or 'applications'.

The new habit, as we shall see shortly, indeed very emphatically had to do with nature, and much the same is true for the object that made its appearance in the same summer, 1926: it was the non-medullated nerve of the spider crab *Maja.* These especially simple nerves only seemingly move us far away from the physiological problems of industrial life, athletes or energetic efficiency, however. This crustacean nerve, it turned out

scientists, Freyling (2005).

379 A.V. Hill (1932a), preface.

380 On bringing the body into the production of scientific knowledge, see Lawrence and Shapin (eds.) (1998); also see Warwick (2003); Herzig (2005).

during these summer months, was *performing* exceptionally well: it 'expend[ed] its energy in nerve activity much more vigorously than does a frog'.[381] More vigorously, this meant, than physiologists' usual, urban tool of choice – the frog's medullated nerves, easily available in the cities; and vigorously enough, moreover, to fall well within the limits of measurement.[382]

If the frog carved out its unnatural existence in urban laboratories, this crab was at home at the Plymouth Marine Biological Station, and thus, at the sea-shores of Devon, interwar icon of British rural idyll, natural beauty and untouched wilderness. Not the metropolis, as Hill had learnt by 1932 was the ideal locale of a physiological laboratory, but 'near the sea, ... within reach... [of] delicate marine animals'.[383] Ideally - the site of Hill's immobilized precision measurement installation, we known, was London. In 1926, however, the Plymouth Station had quite suddenly emerged as an alternative, complementary space – true nature - to these biophysicists' usual, artificial, disturbing surroundings.[384]

Fortunately, as Hill had would lay it out in 1931, at the International Congress for the History of Science in London, the 'development of transport and communication to-day' through *Science* might very well prove more important to history than WWI.[385] Packed in ice, spider crabs, at any rate, were speedily shipped to the capital thanks to the modern night-trains these biophysicists conveniently co-opted. These crabs 'travelled' very well, Hill noted, always arriving in 'good condition', almost as vital and vigorous as if freshly taken out of the water.[386] In terms of the nerve impulse's *heat sign*, such details made all the difference. The vigorous crab not only carried the stigmata of laboratory artificiality far less

381 A.V. Hill (1931a): pp.62-63.
382 On the uses of the frog, see Tansey (1998); and more generally, see F.L. Holmes (1993).
383 A.V. Hill (1932a): p.20.
384 On the rapid expansions of the Plymouth Station in the mid-1920s, see especially Erlingsson (2005); in pointing to interactions between social, cultural and environmental history, my brief analysis of this colonization differs significantly, however, from Erlingsson's account in terms of disciplinary turf-wars. Also see in this connection, Pauly (1988); Benson (2001).
385 A.V. Hill (1932b): esp. pp.275-276; on the background of Hill's appearance at the congress, see Mayer (2002).
386 A.V. Hill (1929a): pp.159-160.

evidently than the frog. It remained shrouded in an air of naturalness.

The crab's vigorous activities exhibited a range of - as far as nerve was concerned - utterly surprising and natural *performances*. Had one hitherto believed, at least until very recently, that nerve was 'essentially fatigue–resistant', the summer of 1926 now finally revealed these believes to be utterly unfounded. Crab nerve, far from being fatigue-resistant, exhibited a 'whole complex' of perplexing phenomena following even brief, intense stimulation: it included very clear-cut signs of something carrying all the signs of exhaustion - 'fatigue'; and notably, it included certain attenuated, 'steady states' of heat production. In the daily life of the crab, Hill quickly discerned, these states presumably indicated a mode of 'economical' use-of-energy on part of the crab.[387] And even so, as Hill enthused, the crab was an impressive exemplar of 'natural excitation'.[388] Unlike the frog, in the crab heat liberation phenomena were easily elicited, and generally required far less of the invasive measures to induce the effect. Equally impressive: much more unambiguously than anything ever obtained with the frog did the crab records reveal a 'clear' division into two phases of heat production,'initial' and 'recovery'.[389]

[387] Esp. Levin (1927); Hill to Fletcher, 1 May 1929, FD 1/2363; A.V. Hill (1929c): p.265.
[388] A.V. Hill (1929a): pp.174-175.
[389] See esp. A.V. Hill (1929a); and A.V. Hill (1932d).

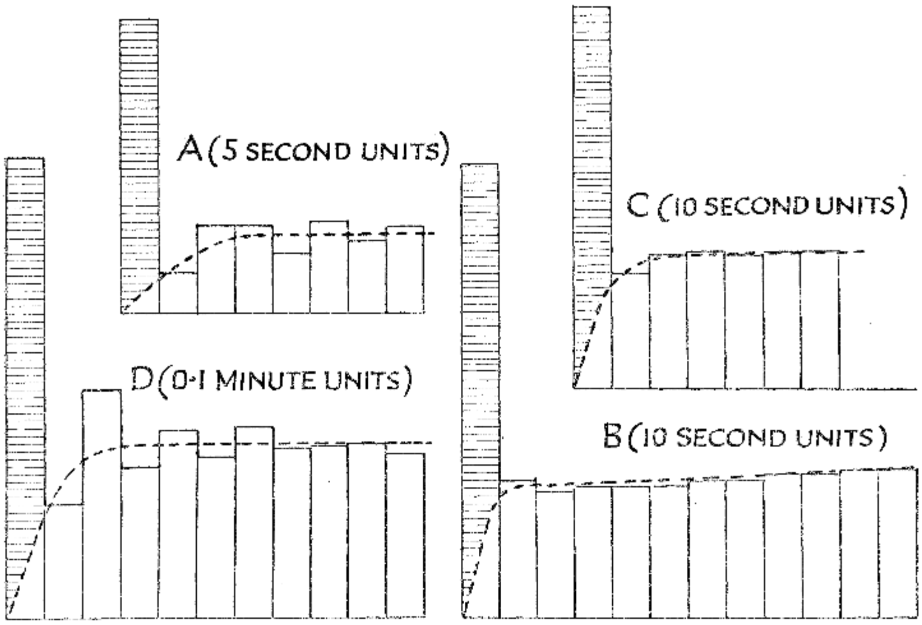

Figure 20: crab vigour, 1928/1929 (note the clearly identifiable 'initial heat')

This nerve behaved, or performed, almost like a little muscle - almost naturally. And none of this was much of an accident. Hill indeed had become 'interested in the question of the possible superiority of some nerves over others for the study of metabolism and heat production' almost as soon as he had arrived at the sea-shores.[390] The energetic revelations of the crab's nerve were the result of a very strategic search for less 'quick', non-fatigue-resistant, more metabolically active types of nerve than the frog's. They were the result, in brief, of a search for nerve that performed even more analogously to muscle – for a nerve that was even more *muscle-like*.

By the mid-1920s such deliberate sampling of the organismic world as such was no longer remarkable. Biologists at the time quite generally were beginning to be very strategic about the inherent and fabricable possibilities of particular organisms and preparations.[391] But the crab implicated something else than matters of technical choice or the standardization processes which historians of biology typically discuss. Not the

[390] Levin (1927): p.114 also see, Hill to Fletcher, 4 June 1925, FD 1/1948.
[391] The articulation of such awareness often is traced to Krogh (1929).

uniformisation of an epistemic space or the knitting together of a community was at issue in this muscle-like nerve.[392] Seeking and finding the crab in the faunal riches of Plymouth was another, complex expression of the model-function of muscular activity. The crab, or its non-medullated nerve, presented, rather successfully so, an attempt at the definite *implementation* of the muscle-analogy. This crab quite plastically illustrates the extent to which the myothermic precedent informed the reality of the heat production of nerve. And in matters of genuine physiological significance, importantly, everything depended on the locale.[393]

This vigorous crab (or rather, its sudden appearance in 1926) was integral to this very modern, mechanic age. The newly flourishing Plymouth Station in due course turned into Hill's cherished alternative venue of experimentation - and of true, if modern nature-experience. The biophysical colonization of this biological beauty spot indeed collapsed with the general mass-touristic disclosure of the area. Earlier generations of physiologists may have sought nature-experience, along with a few others, because it was sublime, heroic or gentlemanly.[394] Hill and his athletic comrades sought nature, along with many others, because they considered it healthy, relaxing and enjoyable. The outdoorsy Hill promptly purchased a little summer 'bungalow' - 'charmante' like 'une petite merveille' - in close vicinity to the laboratories.[395] Not 'altogether … on holiday', here Hill was 'finding the best life', as a nosy reporter was informed at the time, 'with my wife, four children, and my dog, by living in the open air and breathing pure Devon air.'[396]

From the turn of the century, and especially after the war, seasonal settlements, camping sites and bungalow towns had been sprawling along Devon's coastal shores, making it a top priority item for a new breed of tourists, hikers, and campers, alarmed early

[392] Kohler (1994); Rader (2004); Logan (2002); Creager (2002a); Clarke and Fujimura (eds.)(1992); also see Geison and Laubichler (2001).

[393] On the importance of 'place' as a crucial factor in the manufacture of credibility of scientific claims, see esp. Gieryn (2006).

[394] See esp. Felsch (2007); Pauly (1988).

[395] Lapicque to Hill, 7 December 1936, AVHL II 4/52

[396] Daily Express (1928) quoted in A.V. Hill (1960b): pp.150-151.

environmentalists and interwar guardians of rural England alike. Motorways, rail tracks, bridges, cars, buses, bikes, and overland lines encroached upon even the remoter hinterlands; coach and railway companies began to offer 'rambler tickets' and special train services departed to Devon's beauties from the major cities on the weekends (for the especially neo-romantic, at midnights).[397] Like the *natural* excitation of nerve, the nature that was Devon was *crafted*, shining from railway posters, tourist brochures and advertisements in magazines; and all the while, Devon was moving closer to the capital and its leisure-and-nature-seeking inhabitants - Hill included.[398]

To London biophysicists, Plymouth meant, quite emphatically so, the antidote to their mechanic, urban experimental lives: a place where one could acquaint oneself with the 'biological truth, ... [and] the biological standpoint'. There it was possible to escape the necessary, 'extreme specialization at intervals' by means of which 'discoveries and progress [were] made' in this present age. And still, as Hill ventured in front of a student audience in 1931, 'their bearing is best seen by letting the engine run idle and giving oneself the time to look round.'[399]

By then, Hill and collaborators were routinely migrating, each summer, to picturesque Devon. Plymouth meant more than the sum of its parts - pure air, idleness, and a rich fauna and flora. It was the total experience that counted, and Hill would turn it into a programme, habit and annual ritual, henceforth guiding his scientific friends, collaborators and students to the Station. At Plymouth, Hill's men were to soak up true biology and nature life – become 'properly equipped'.[400] Indeed, it was 'happy times' as one of them, Rudolfo Margaria, formerly the director of the High Altitude Research Station on the Col d' Olen (Monte Rosa), would reminisce of these days: 'sleeping under the tent,

[397] On the limitations of any such stereotypes, see Trentmann (1994); and especially Mandler (1997).
[398] E.g. Smiles (1998): pp.7-10; Walton (2000): esp. pp.34-36; more generally, see Hassan (2002).
[399] Quoted is Hill (1931), in A.V. Hill (1965): p.44; also see A.V. Hill (1960c): pp.17-18 and Hill to Fletcher, 3 June 1926, FD 1/1818; Hill to Fletcher, 27 September 1926, FD 1/1948; Hill to Denton, 30 August 1948, AVHL II 4/20.
[400] Hill to Fletcher, 3 June 1926, FD 1/1818; Hill to Fletcher, 27 September 1926, FD 1/1948; on a break-down of visitors see Erlingsson (2005): p.115.

being woken up by the children pushing a cigarette in my lips, then going for a run, and all the rest.'[401]

The result of a kind of strategic, urban escapism, in the midst of these natural surroundings, radiating its biological truth, the crab's nerve had made its incisive appearance. Crab nerve, it was plainly visible on the records, liberated heat intensely, unquestionably, naturally, even after travelling to the city. The heat sign made its definite appearance as a compromise between nature's unspoilt manifestations and certain technological requirements, between the shore and the city: natural phenomena there, technologies of precision there, connected by means of modern transportation.

There was what seemed a real, genuine, and natural physiological *fact*. But there was, of course, more to come. This fact unquestionably implicated, in analogy to muscle, in analogy to the athlete, some cyclic, oxidative, energy-consuming *process*: natural, and well-nigh universal. '[W]e deceive ourselves', Hill will thus conclude his *Chemical Wave Transmission in Nerve* (1932), easily one of the most influential treatises on nerve penned between the wars, 'if we do not recognize behind [heat liberation] a cycle of molecular change in the nerve'.[402]

At the very gates between life and death

Oxygen debts, steady states, energetic stores, heat liberation, and explosive *changes* came together in the late summer of 1928, roughly two years after the first successful measurements of nerve heat, two years after the vigorous spider crab had appeared on the scene, some five years after the phenomena of oxygen debt had first been exposed in athletes, and many years after Hill's first forays into the heat liberation of muscular activity.

401 Margaria to Hill, 23 July 1946, AVHL II 4/58
402 A.V. Hill (1932a): p.35.

The daily Press then descended 'like an avalanche' on Hill's Devon summer refuge. Hill, or so one could read it in the newspapers all through September, had made an important discovery 'at the very gates between life and death'. The 'inner citadel of the mystery of life' had been exposed.[403]

The avalanche had been unleashed by a 'public lecture' (and 'some very exaggerated statements') by Frederick Donnan at the BAAS meeting in Glasgow earlier that month.[404] Donnan, whom we already have met in chapter 1 as an acclaimed membrane specialist, had chosen at his topic the 'first great problem, perhaps the only great problem ... [and] the true task of biology to-day'. Namely, the living cell, and therefore, what was 'in reality a ... dynamic equilibrium'. Donnan's exposition of this 'Mystery of Life' reached its climax in a discussion of some recent experiments of Hill's, and thus, he ventured, the central mystery of them all, the maintenance of life and the nature of 'cellular death'. It was a dramatic picture of 'constant oxidation' that Donnan presented to his audience: for the 'first time in the history of science we begin, as yet a little dimly, to understand the difference between life and death'.[405]

Indeed, since 1926 the heat liberation researches had taken some unexpected turns. The crab was only one of them. There were more: slowly but gradually, energetic conversions had emerged in the hand of Hill's biophysical troupe as the chief determinant as regards nervous action - tout court. In 1927 one had first discerned a curious diminution, or saturation, of the *heat-per-impulse* as one went for ever more drastic means of intervention so as to give, as was deemed absolutely mandatory, 'further definition' to the heat-sign: stimulation with rapidly alternating, high-frequency currents.[406] Above about fifty shocks per second, delivered with a new, purpose-built rotating commutator, the liberated energy suspiciously and suddenly levelled off quite drastically. It pointed, or so it was

403 A.V. Hill (1931a): pp.9-10; nn. (1928); and see the recollections of Hill's wife in A.V. Hill (1960b): pp.148-155.
404 McSwiney to Hill, 25 September 1928, AVHL II 4/57
405 nn. (1928).
406 see Gerard, A.V. Hill, and Zotterman (1927).

reckoned in London, unquestionably to the compound presence in the data of two phases: a relatively constant heat liberation due some permanent, continual 'recovery process' and a 'rapid outburst' of heat production.

Under these conditions of severe *exercise,* for anyone immersed in the science of athletic performance and thus, tuned towards discerning extreme performance in extreme conditions, this initial heat here must have very naturally emerged as the fundamentally dynamic state of a 'capacity' for heat liberation: a state continually on the 'return to [complete] energy liberation'. [407] Indeed, even more perplexing results were promptly supplied by Hill's co-worker Gerard. Only shortly later and by means no less drastic, Gerard exposed the presence of nothing less than an 'oxidative reserve' in the frog's nerve.[408] Again, it required an extreme environment - immersion of the nerve in nitrogen – so that these energetic stores manifested themselves as peculiar, attenuated, 'constant' states of energy liberation. This condition of endurance – ongoing, diminished nervous actions - though reminiscent of a state of fatigue, more aptly would be called, as Gerard pondered, an 'equilibration'.[409] These performances under extreme conditions, were genuine, tissue-level steady states - dynamic equilibria.

All this may seem trivial, and indeed it was – for everyone, that is, *already* operating in a space - as did Gerard, as did Hill, as maybe we do – where nervous action was an intrinsically metabolic, energetic, muscle-like affair. But exactly this was not trivial at the time. It was only recently, I have shown, that a fine-grained, practical vision of energetics had become virulent in the world of muscular *performance*. Everyone of Gerard's interventions was indeed guided by this vision - the notion that nerve would behave in ways 'analogous' to muscle.[410] And still: as far as isolated organs were concerned, nothing in the way of such energetic stores had been exposed before.

[407] Ibid., esp. pp.140-142.
[408] E.g. Gerard (1927c): esp. pp.401-403.
[409] See esp. (1927): p.497.
[410] See esp. Gerard (1927b): p.280; (1927): pp.496-497.

Accordingly, above 'store' manifested itself, or so it seemed at first, as a clear *deviation* from the analogy of muscle. As Gerard found to his surprise, depriving the nerve of its oxygen-supply - a routine procedure in muscle physiology - did *not* result in the instant 'failure' of the recovery process as would have been the case with muscular machinery.[411] Instead, quite *unlike* muscle, the 'failure' of nerve was a gradual, protracted, slow accumulation of an 'oxygen debt': the progressive depletion of an oxidative reserve on which the impulse 'ultimately' was dependent. But until then, like it or not, the nerve settled into a peculiar state of continual activity, debts were incurred, and ultimately - or *failure* would yield to *death* - it would have to be paid back, that was, restored.

What had appeared as an irritating anomaly at first - the fact that the details of a nerve's *failure* process deviated from the analogy of muscle - upon closer inspection was revealed, by Hill himself, as a deeper, fundamental likeness. Prompted by Gerard's results above, still in 1928 Hill uncovered, spectacularly, and under similar conditions of 'extreme exhaustion', a persistent, steady-state 'increment' in the heat production of muscle during rest. Its nature, presence and ultimate oxygen-dependence and presence was, and this was the real drama, inexplicable in terms of lactic acid formation - i.e., the normal, anaerobic mechanism of muscle.[412] Meanwhile, the implications - soon to be dramatized by Donnan - were essentially the same.

As with Gerard's nerve, and despite the extremity of both, intervention and condition, these were, as Hill took pains to demonstrate, not only 'genuine' physiological effects. These steady state phenomena pointed, like a nerve's persistent performance, towards the 'definite and material' existence of 'large amounts of energy' stored away in the living tissues the release of which was 'normally' inhibited.[413] 'Cut off' the oxygen supply, and these energy stores would be unleashed, making 'previously ... impossible'

[411] Gerard (1927b): pp.295-297; (1927): p.496.
[412] A.V. Hill (1928b); and A.V. Hill (1928a): esp. p.76.
[413] A.V. Hill (1928b): pp.106-107.

reactions possible. And, in the continued absence of oxygen, so Hill, a cell invariably went down the path of destruction: dissolution, biochemical 'chaos', and finally, death.[414]

Between nerve and muscle, between the performances of isolated organs and the whole man, between London and Devon, here had been exposed the 'very fundamental', indeed all-important 'role of oxidation in maintaining the dynamic equilibrium' of excitable tissues.[415] Such dynamic equilibria were real - universally manifest in phenomena stretching from palpable athletes to muscle to delicate nerve.

The impulse as such, its 'essential reaction', this also meant, would be an energy-consuming event.[416] All this, surely, was bad news for anyone still adhering to a purely physical conception of the nerve impulse. But as surely, nothing here was a foregone conclusion either. We have seen how all along estimates for the explosive change, the initial heat, dwindled towards nothingness; alternative interpretations, it also had to be admitted, might well still be possible; and if anything, these new horizons were predicated on even more invasive, more artificial means of *exercising* the tissue. Yet, for those moving among Hill's circles, and the numerous others tuned to a world of muscular motion and efficiency, it took little to discern underneath these diagrams of heat production a whole new realm of natural, genuinely physiological non-equilibrium phenomena: failure, advanced fatigue, extreme exhaustion, oxygen debt, steady states, economic energy expenditure and more. The model-function of muscle-activity had found its fundamental expression. And having explored this world of activity, efficient motion, and bodily performances, this is no longer surprising: the men who crafted it were men alert to the concrete and physiological problems of modern living - extreme performance under extreme conditions.

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414 Ibid., p.160.
415 A.V. Hill (1928b).
416 Gerard (1927c): p.396.

Conclusions

The events that followed, intersected and paralleled the dramatic summer of 1928, when there first dawned a detailed outline of an energetic picture of the nervous impulse, we essentially have covered already. It continued, along many routes, the project of stabilizing, defending, and giving further definition to these muscle-like performances of nerve: the impulse as an explosive outburst of heat - cycles of exhaustion, restoration, and outburst again. And no single item as such had made the phenomenon real and genuine. But spun together, the naturally vigorous crab, the frog (when extremely exhausted), the analogous phenomena in muscle, and the palpable, skilled, oxygen-debt incurring athlete by the early 1930s left little room for reasonable doubt.

It was this web of things, palpable analogies and phenomena that made the initial heat very real indeed. Detailed pictures of the putatively underlying chemical machinery, tightly modelled on the nuanced physiology of muscle, would soon be advanced notably by Gerard as well as by Hill himself. The latter even supplied a detailed, formal reconstruction (a 'simple mathematical deduction') of the temporal dynamics of the various *phases* that putatively composed the heat sign. [417] Hill's hugely influential *Chemical Wave Transmission in Nerve* (1932) presented this grand vision of an essentially energetic, active, and chemical nature of nervous conduction to a much wider audience. This vision, to be sure, wasn't complete, but not missing quantitative, biophysical rigour either; and it was full of analogies, models and pictures that reinforced its status as something genuine and real - most notably, of course, the 'Analogy of Muscle'.[418] This vision bore little resemblance with the vision Hill himself and a great many other physiologists had sported still less than ten years ago, when it had seemed plausible enough that nerve was essentially 'fatigue-resistant'.

[417] Gerard (1927): pp.498-499; A.V. Hill (1932d): esp. pp.106-110.
[418] Also see A.V. Hill (1932a): esp. pp.35-37; A.V. Hill (1933c); A.V. Hill (1933b).

No longer. What remained was the fundamental nature of the problem. Nothing was settled. Hill's entire, ensuing campaign for the recognition of these energetic, 'wave-like impulses' was indeed framed as a biologist's 'S.O.S.' to engineers, chemists and physicists.[419] But one of the things this chapter has shown is how essential it is not to misread such statements in terms of the 'cultural hegemony' or 'colonization' narratives of the incursions of physics into biology.[420] Neither was Hill simply a pioneer and far-sighted promoter of 'biophysics'. Here (as elsewhere) Hill was lamenting, thoroughly in line with his general biological optimism, the 'disgraceful' 'ignorance and pride of otherwise educated people' in matters of biology rather than advancing colonization or some narrow, reductionist view of a would-be discipline biophysics.[421] Indeed this chapter has shown that a very different picture of this biophysical pioneer emerges when we take seriously the historical circumstances that shaped this type of physiological work - and its objects - at the time. Hill's scientific enculturation in Cambridge certainly was crucial in this connection; but so were his services to the IFRB in matters of athletic skill or the annual migrations of London biophysicists to Plymouth. The neuromuscular body, the practical, biomedical problems it was perceived to implicate, were central to shaping Hill's bio-physical science, and they were central to reshaping the energetic vision of nervous action as well.

This focus on the body, like the dichotomies between the idyllic, touristic Plymouth and urban London I have painted, invoked a most clichéd and far from unproblematic historical image of the interwar period, but here it was advanced for a purpose. The importance in this story of the peripheral nervous system, the athletic, neuromuscular body, and of the practices surrounding it, certainly betrays the limitations of the mind-and-brain-centredness of current neuroscientific historiography. Likewise, as was the case with

419 A.V. Hill (1932a): p.viii.
420 See esp. Abir-Am (1982) and the ensuing reactions in Vol. 14, No. 2 of Social Studies of Science (1984); also see Fox-Keller (1990).
421 Cited is A.V. Hill (1932b): p.275; also see A.V. Hill (1933a); A.V. Hill (1931c).

cellular surface behaviour in chapter 1, the shift from 'passive' to 'active' conceptions of physiological processes here appeared not as a matter of intellectual history and bio-philosophical positions, but as an expression of practical, material conditions and problems.

The model-function of muscular activity – the physiological of isolated muscle as much as the figure of the athlete - *mediated* in ways much more concretely a novel, active, and vital picture of the energetic manifestations of nervous activity. Again, it was things that mattered. Not *ersatz* in this case, but a historically specific spectrum of crafted, natural *performances*. Both this impulse and its science, I have shown, formed around and between a set of pressing, concrete, and palpable concerns - things everyday and real enough: muscles, bodies, athletes, nature, health, the physiologies of industry, exercise and efficiency. As in the previous chapter, the correlate was a form of biophysical knowing that was both local and non-local, and deeply entangled in contemporary life-worlds.

Indeed, the nervous heat production evaporated almost as suddenly as it had made its appearance on the Easter Sunday of 1926. It was only for a short time span around 1930 that this transient constellation of muscles, bodies and applied physiologies sustained nervous behaviour as an energy-consuming, muscle-like, living non-equilibrium process. A last and extensive review of the field, written in 1936 by one Chinese assistant of Hill's, concluded with a note on the exhaustive degree of 'perfection' that had been achieved in matters of electrothermometry - room for further improvement 'seem[ed] to be narrowly limited'.[422] Room for progress opened up in other spaces and landscapes. As we shall see in the chapters to follow, in parallel and even more so, subsequently, more powerful and more promising seeming *electronic* techniques largely came to define the study of cellular behaviour. The quest for underlying 'events' did not abate, but towards the middle of the century increasingly little would remain of the cohesive fabric explored in the present

[422] Feng (1936): p.129.

chapter: the cultural and ideological alliance of nerve and muscle physiology, industrial society, and peripheral nervous system. Gradually, but persistently, the central nervous system emerged as the *discursive centre* of neurophysiology. Meanwhile, even the vigorous *performance* of 'isolated organs' would lose its natural appeal to investigators. Isolated organs were displaced as novel, *single-cell* recording techniques turned hegemonic. Along with the broader transformations of electrophysiology's material culture to which we now turn, these electro-technological environs made salient neither performances nor chemical, metabolic events. They served to re-prioritize again an essentially electrical, physical vision of the impulse.

The heat production of nerve was never discredited intellectually, however. Its substance was essentially thing-bound, real and present in historical circumstances where muscular performances mattered. Palpable and widely visible at the time, as the practices, things, and performances which surrounded it withered, largely withered the phenomenon of heat production.

(3) CIRCUITS.

Excitable tissue in the radio age

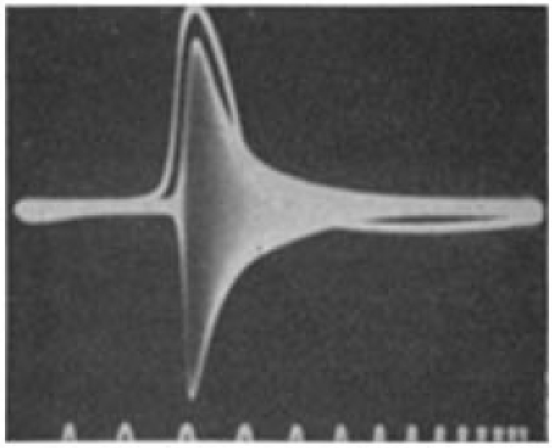

Figure 21: Impedance change, 1939

Figure 1 is a photograph taken of the flickering surface of a cathode ray tube screen; the tube connected, via a multi-stage amplifier, to a micro-electrode; the electrode, in turn, carefully inserted into the interior of a squid giant axon. The record taken shows the change of resistance, or to be precise, the *impedance*-change of the axon during the passage of a nervous impulse.[423]

The impulse left this particular imprint sometime in summer 1939, under the

[423] Impedance = AC resistance.

watchful eyes and in the hands of Kenneth Cole, Assistant Professor of Physiology at Columbia University, and his colleague, the biophysicist Howard Curtis. Here was produced, on a lab-bench in Woods Hole, Cape Cod, the kind of intimacy and directness the *heat index* seemed to be lacking. There were no artificial *imitations* involved in this particular production, but a real (if unusually large) nerve fibre. And indeed, this chapter will lead us onto seemingly more familiar terrains as far as the nature of the cellular behaviour is concerned. But, this chapter argues, even these seemingly familiar terrains of real nerve and natural nervous behaviour reveal themselves as far less familiar landscapes composed of electrical bodies and artificial, man-made circuitry. This chapter, like the remaining ones, will be concerned with the *fabrications* of the nerve impulse as an electrical event.

As to this event, the record reproduced above was not just any record. The *New York Times* reported that quite possibly, one had found the 'Rosetta stone for deciphering the closely guarded secrets close to the very borderland of mind and matter'.[424] For the first time, at any rate, there was recorded in these experiments by Curtis and Cole's a change of electrical resistance of the nervous membrane – by *direct* means, and *during* activity. So stalled in time, the tracing has become iconic since. Reproduced countless times, in publications, text-books and these days, on websites, it has come to signify, to serve as a stand-in for, nervous activity quite generically. And clearly, it would be tempting to inscribe this tracing into an iconology of bioelectrical transientness which would reach back to the earliest days of electrophysiology - graphical renderings of passages leading from *negative variations* to *propagated disturbances* to *spikes* - from Matteucci and Du Bois-Reymond to Bernstein, and from there to Keith Lucas, Douglas Adrian, Gasser and Erlanger and eventually to figure 1 and on to neuronal codes and signals; and thus, to fold it into a succession and generations of inscription devices, from mechanical to electronic ones -

[424] nn. (1938): p.35.

from frog rheotomes to galvanometers, capillary electrometers and finally, cathode ray oscillographs.

Tempting, to be sure, and not so much wrong than historically one-dimensional and uninformative. One reason, we shall see, indeed is this: although we know of the impulse, certainly in historical terms, largely as a two-dimensional *inscription*, pictures, images, graphs and curves are problematic sources. Of course they always are, as historians of scientific images have amply demonstrated, the end-products of complex fabrication processes. But as such they can suggest historical similarities, superficial likenesses and continuities when there were none. And in prioritizing the act of recording, the permanent, and the visual, they foreground certain scenes, sites, practices and issues while obscuring others.[425] One thread running through this chapter is the extent to which this most paradigmatic subject of inscription devices - the electrical impulse – did not collapse with, and wasn't exhausted by, a history of the graphic method and its various derivatives. Instead of an exegesis of traces, this chapter exposes the mundane, material substrate of nervous behaviour behind - as well quite apart from - its traces and inscriptions.

This chapter, that is to say, too presents a variation on the theme of modeling by way of *ersatz*. Or to be precise, it presents an account of the models and the technologies of interpretation that made biophysical interventions - whether or not they resulted in visible traces - transparent, intelligible, and readable. In doing so, this chapter will take as its starting point not even the practices of image-making, but the practicalities - and the very materiality - of these technologies of biophysical interpretation. In concrete terms, the legibility of tracings such as Cole and Curtis' above thus was predicated on a particular form of model, a so-called 'equivalent circuit' such as this one:

[425] The pertinent literature - now subsumed under the 'visual turn' in the history of science - is, of course, huge, for some more programmatic statements, see esp. nn. (2006); Pauwels (2006); Daston and Galison (2007).

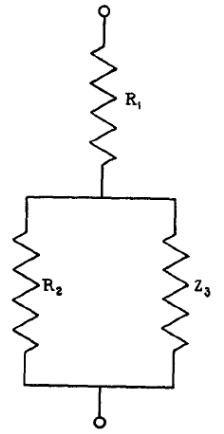

Figure 22: equivalent tissue circuit, 1932

Depicted is a structure electrically 'equivalent' to a biological cell - a cell, that was, by implication 'behaving' 'as if' it was composed of resistances and condensers.[426] In the hands of Cole and Curtis, such artificial circuits were geared, as we shall see, towards probing the structure and nature of the cell membrane. Significantly, however, their uses were many, and the scenes from where they originated, I shall argue, are indeed not the scenes familiar from the historiography of neurophysiology.

Like Cole and Curtis themselves, this morphology of circuits will move us beyond the usual focus on local, academic contexts, Nobel laureates and pioneers such as E.D. Adrian who belonged to the first to employ the vacuum tube productively in the electrical analysis of nerve.[427] Instead, these circuits will lead us into the highly technical borderlands of physics and medicine that took shape as practices ranging from x-ray diagnostics to electrocardiography to UV light therapy firmly took root in hospital departments and private practice alike. These were key sites, I shall argue, of biophysical knowledge production in virtue of their assembling physical agents and biological things: here one administered, controlled, gauged, intervened, dosed, effected, and most of all, measured.

Emergent from such mundane, electrified practices – again - was a distinctive form of modeling. And accordingly, these circuit *equivalences* were not a matter only of drawings

[426] This particular one comes from Cole (1932).

[427] Esp. Marshall (1987); J. Harvey (1994); Bradley and Tansey (1996); Millet (2001); Tierney (2002); Magoun (2003); Borck (2005); Borck (2006).

on paper. In many cases, as we shall see, knowing and analysing an unknown thing *electrically* thus simply but very concretely meant making it part of a circuit: finding, that was, for an unknown circuit element (such as a nerve) a circuit element of known properties and analysing the latter. And either way, such knowing-by-substitution was next to mandatory when it came to bioelectrical measurement. Many years later, in a 1950 textbook on *Research Methods in Biophysics*, Curtis would describe the signal importance of such supplementary activities in the following terms:

> In general it is important to draw the equivalent circuit for one of two reasons. The first is to prevent errors of measurement and to make sure that the measurements actually represent what they are supposed to. The second is to aid in the interpretation of the measurements.

'Failure to do so' was bad practice, while 'many apparently puzzling phenomena appear quite simple when analyzed in this elementary way.'[428] Inscriptions were not to be trusted, or in any case, remained illegible otherwise. The hands-on, practical, and material interminglings of circuits and cells indeed is the second key theme of this chapter: an ontology of circuits (to exaggerate only slightly). For, the cultural resonances, the imagery and metaphorology of circuits are broadly familiar, of course, whether we think of the analogical traffic between the telegraph and the nervous system in the nineteenth century or later, the resonances during the 1920s and 30s between wireless 'media' technologies and the electrified brain as analysed in Borck's cultural history of the EEG, or still later, the cybernetics movement of the 1940s and 1950s.[429] The present chapter goes much further, however, in anchoring this mode of biological knowing in the electrified, technology-infused interwar life-worlds of Western industrial society. Unlike the nineteenth century, when electro-magnetism was an exotic, utopian, or at best, an urban and elite experience, these were worlds increasingly suffused and replete or even, 'congested', as some

[428] Curtis (1950): pp.235-236.
[429] See esp. Otis (2002); Borck (2005); Hagner (2006): esp. 195-222; Abraham (2003b).

contemporaries diagnosed, with wirings, cables, networks, and electrical gadgets and commodities.[430]

Far from being confined to particular spaces, knowledge of electrical things was common knowledge, bordering on a form of cultural technique - 'every child dabbled of resonance, filter circuits and distortions', as one German physiologist recorded.[431] And again, a case will be made for the crucially concrete and material rather than verbal and metaphoric dimensions of such electrical *models*. We may speak of them as analogies-in-use, or technologies of interpretation, for they were, as we shall see, developed in response to problems of a practical kind: to make biophysical interventions, whether they occurred in the laboratories or the clinics, transparent and readable. Bioelectrical *ersatz* was quite literally a question of substitutions: of turning organic tissue into circuitry. The kind of modeling practice at issue will reveal themselves as deeply enmeshed in interwar electrical life-worlds - conceptually, culturally, and materially.

This electric world?

By the time Cole and Curtis traced the passage of the squid impulse, the 'glimpse into the electrical processes of a billionth second' was turning into a visible and visual reality, quite generally. Such ubiquitous, everyday phenomena as 'the switching process' – still 'cloaked in mysterious darkness' but familiar to everyone 'pressing the buttons of a telegraph, switching on light bulbs and engines' - would soon be exposed, as one electro-engineer enthused in *Naturwissenschaften*.[432] The basis of such wonders, the vacuum tube, had now definitely emerged as a cheap and modern, universal 'electrical lever', or so celebrated the journal *Electronics,* newly launched in 1930: 'There will be nothing that the average man sees,

[430] Cited is the piece Under London (1939), quoted in Otter (2008): p.243.
[431] Ranke (1941): pp.1-2; on this point, also see Hughes (1998); and Wurtzler (2007): pp.88-101.
[432] Rogowski (1928): p.161.

hears or buys but what will be controlled, regulated or affected in some important respect by an electronic tube!'[433]

Advances and improvements in the 'electronic arts' had not least affected what was seen and heard by the biological scientist. 'The advent of ... vacuum tube amplification', as Cambridge physiologist Adrian surmised, 'has so altered the whole position that we can compare ourselves to a microscope worker who has been given a new objective with a resolving power a thousand times greater than anything he had before.' [434] Henceforth, one chased the 'immediately correct inscription' and 'true picture' of the transient manifestations of bioelectricity - not with mechanical devices, but at the speed of electrons.[435] 'It [was] only fair', as Adrian also surmised, to point out how recent progress in nerve physiology has 'depended on the very modern comfort of broadcasting'.[436]

Interwar physiologists were more than quick to speak of a 'revolution' when it came to amplifying powers of wireless gadgetry even as there was no lack of the more sceptical voices.[437] To be sure, as the historians of neurophysiology Frank and Borck have argued, this rhetoric of revolution is deeply problematic concealing both the extent to which ficklish electrical apparatus fell short of being revolutionary; in particular, how established, local patterns of experimentation crucially impinged on the given incarnations of physiologists' newly electrified experimental systems and their scientific productivity.[438] And still: *local* culture and style are only one set of criteria to bring to bear onto this unquestionable transformation - sheer scale, breath and electrical mundaneness quite another. The following is not much interested, accordingly, in whether or not wireless technology shaped the character and details of this or that neurophysiological venture; it is interested instead in the broad-scale condensation and concretion of electrobiological

433 Caldwell (1930): pp. 10-11.
434 Adrian (1932a): p.5; and see Cremer (1932): p.270; p.279.
435 Rosenberg (1930): pp.120-121.
436 Adrian (1928): p.39.
437 E.g. A.V. Hill (1922); Forbes, Davis, and Emerson (1931): p.2; Adrian (1932b).
438 See Frank (1994); Borck (2006).

phenomena around these newly ubiquitous electrical technologies and modern comforts. By their very systemic, compositional nature it would be difficult to conceive of electric things as a unidirectional force. Nor were neurophysiology (or electrophysiology) stable or clearly delineated fields of inquiry at the time. What I *shall* argue is that the electrical fabrication of the nerve impulse needs to be seen as part of a much broader reformatting of vital phenomena in the context of the pervasive techno-cultural everydayness of electricity.

For there can be no question: in the wake of WWI and on an extent not even remotely charted historically, biological scientists, physicists, chemists, electrical engineers and radio hobbyists in England, Germany, France and the USA simultaneously began to struggle with the newly available wonders of wireless.[439] In an heroic (and rare) effort to provide a comprehensive account of the electrobiological progress Hans Schaefer's *Elektrophysiologie*, finally completed in 1940, even felt prompted to develop a new bibliographic system; not even counting in the 'purely clinical-pathological' studies, topics of a mostly electrochemical and electrophoretic nature, the 'physiology of short-waves' and of 'high-voltage currents', and 'all those things where the electrical [was] only *Technik*', Schaefer's two-volume tome - strategically confined to the more 'theoretical' aspects at that - still included more than 6000 references - 100 publications in 1921, the foreword gasped, 200 in 1927, more than 500 in 1938.[440] Indeed tracts such as Schaefer's (*Elektrophysiologie* was soon accompanied by similar, nerve-centred treatises) are illustrative not only for what they actually managed to include after all, but for what they excluded – explicitly acknowledged or not.

The many *Randgebiete* – the borderlands – which Schaefer only gestured at in the above have subsequently been obscured, just like muscles, bodily movements or colloidal

439 Electronic instrumentation has received fairly little attention by historians of science, but see Baird (1993); Hughes (1998); Haring (2006).
440 Schaefer (1940): p.IV.

phenomena by the newly coalescing field of neuroscience and its nervous-system-centred, selective memory - of which works such as Schaefer's marked a beginning rather than an end.[441] But, it were these *Randgebiete* - from Schaefer's nerve-centred perspective - where the long-standing metaphoric alignment of nervous system and electrical telegraphic technology was transformed into a materially and culturally embedded radio-technological practice of modeling. Or this is what this chapter is going to argue. The more familiar scenes of classic, academic nerve physiology which have dominated the few accounts we actually do have of interwar physiology, in turn, will receive no particular attention here: Adrian, Sherrington, Dale, Cannon, the *axonologists*, and the story of the war between the 'soups' and 'sparks'; they only formed part of a much vaster world of bioelectrical knowledge production.[442] Let us now de-centre the picture first, and then re-approach Cole's tracing, the one reproduced at the outset, from these borderlines.

We have already seen that and how it is possible to paint very different pictures of cellular behaviour than the more familiar ones: pictures that take as their starting point the very diversity of biophysical projects, and their concrete, thing-centred rather than their philosophical, institutional or purely academic driving forces. The frustrations a Warren Weaver experienced with biophysics at the Rockefeller Foundation, as highlighted by Robert Kohler, shouldn't distract from the plethora of indeed quite feral activities in matters of biophysics.[443]

This is perhaps particularly true for the interwar *biomedical* fascination with physical effects on biological things – and the tinkering with them. Consequently, the present chapter too will be concerned with a range of biological materials and the mysterious

[441] See foreword to Schaefer (1940); the flurry of monographs on nerve physiology at the time, notably included Katz (1939); Muralt (1945); Lorente de Nó (1947); J.C. Eccles (1953); Brazier (1961).

[442] The Sherrington hagiography is fairly extensive, see e.g. Granit (1967); Swazey (1968); J.C. Eccles and Gibson (1979); but see especially the work on Sherrington by Smith, e.g. R. Smith (2001a); on Cannon, see esp. Wolfe, Barger, and Benison (2000); Dror (1999); 'soups' and 'sparks' were popular shorthands in the 1930s to refer to controversies revolving around pharmacological vs. electrophysiolocal conceptions of synaptic transmission, see esp. Harrington (2008); Bacq (1974); Dupont (1999); Valenstein (2005).

[443] Kohler (1991): esp. p.299.

effects upon them of *physical* agents that spilled well over the merely nervous. As much as electricity and electrical things began to pervade everyday, modern lives, bioelectrical knowledge was generated by a whole spectrum of excitable tissues ranging from patients to algae to nerve and muscle, as we shall see. And we shall see how these borderlands were entangled and mutually intersecting rather than isolated domains.

This inclusive view on things electro-biological and thus, medico-physical, is central to the following. As Robert Bud has pointed out in his study of penicillin, in terms of medical body-awareness, the interwar period were deeply distrustful towards anything *chemical*.[444] In contrast, physical agents – heat, sun light, radium, electricity – were clean, modern, natural. This intense fascination with the physical found institutional expression in venues such as the Frankfurt Institute for the Physical Fundamentals of Medicine, the Vienna Radium Institute, or the Johnson Foundation for Medical Physics in Philadelphia, the latter launched in 1930 and directed by one of Hill's most cherished pupils, the engineer-turned-biophysicist Detlev Bronk.[445] Less visible were the many smaller-scale biophysical ventures, local collaborations, or the innumerable hospital departments devoted to physical therapy, electrocardiography, x-rays, and electro-medicine.

'[N]ew and highly technical' methods of diagnosis and treatment radically changed the face of medicine, or so the rhetoric went, fuelling not least the many calls for curriculum reform in the medical sciences.[446] These environments were as heterogeneous as they were generally eclectic, service rather than research oriented, and driven by technical application and enthusiasm not by any overarching disciplinary goal or intellectual agenda. The correlative of the environments thus created, spaces carved out at the borderlines of medicine, biology and physics was an experimental life characterised by a culture makeshift and improvisation, and opportunities chanced rather than designed. It is this feature that

444 Bud (2007): chapter 1.
445 E.g.Dessauer (1931); Rentetzi (2004); Cooper (1984).
446 Cited is Dean, 'A review of the medical curriculum', (1930), ROUGHTON/APS, Box 34.60u; also e.g. H.B. Williams (1929); Rockefeller Foundation (ed.) (1932); more generally see Simon (1974); Sturdy (1992b); and esp. Weatherall (2000).

makes them relevant to the following. For our purposes, and to enter these vast and wired terrains, the case of Hugo Fricke (1892-1972) will be especially instructive. His researches into electrical properties of biological materials intersected deeply, as we shall see, with the electrical vision of the nervous impulse that was in the making. As such, Fricke's biophysical oeuvre was grounded in practical matters. Indeed it was emergent out of the form of biophysical normalcy at issue here.[447]

More than a A.V. Hill, the Nobel prize winner, or a Bernal, leftist 'sage' and womanizer, does Fricke exemplify the typical interwar biophysicist - a technical worker rather than an outstanding figure. But neither was Fricke disconnected from the biological world at large; or rather, he didn't remain so always.[448] When in 1928 the Cold Spring Harbor Laboratories were scouting for a director for their projected programme in biophysics, the advisory committee thus settled, eventually, on one Hugo Fricke.[449] Trained in engineering and physics in Denmark, Fricke had been taken on as a research assistant in physics at Harvard in 1920. The year later, however, Fricke was diverted by the famous surgeon George W. Crile. Crile was busy launching a new and ambitious biomedical venture, the Cleveland Clinic Foundation.

Fricke was to direct what was at the core of Crile's vision, the biophysical laboratories. Crile, meanwhile, already had his biophysical epiphany at least twice. First, in 1887, when Crile witnessed the death through 'shock' of a fellow student whose legs had been crushed by a street car ('the dramatic picture of failing bodily energies and death'). And again, when Crile, as the surgical director of the American Ambulance, witnessed the 'intensive application of man to war' at the Western front.[450] Millions of similar cases of 'shock – a violent restless exit', as he reminisced. In the process, Crile disclosed blood transfusion as the most effective treatment for shock, a subject that quite generally proved

[447] On Fricke, see A.O. Allen (1962); Hart (1972).
[448] On Bernal, see A. Brown (2005); also see Berol (2000).
[449] Harris to Fricke, 16 October 1928, FRICKE/CSH, folder 'Dr Hugo Fricke' (3/3)
[450] Crile (1926): p.3.

something of a biophysical rallying ground.[451] A renowned transfusion pioneer himself, Crile remained at a loss, unable to identify what happened 'within the cells themselves in shock and exhaustion.'[452] Cramming treatises on electricity, pondering the 'physical interpretation of the energy transformations of cells', and already convinced, anyhow, 'that man and other animals are physico-chemical mechanisms', still in 1917 Crile therefore initiated a series of biophysical investigations into the electrical conductivity of animal tissues. Co-opting the special expertise of Miss Helen Hosmer of the General Electric Laboratories, the basement of his Cleveland home served as the temporary base: by the time the war was drawing to an end, Crile and his Cleveland based-team had converged on the conclusion that shock was 'marked' by a diminished conductivity especially of the brain, and an increased conductivity of the liver.[453]

The 'organism', Crile then inferred, was 'operated by electricity'.[454] Crile lost no time organizing a Department of Biophysics around investigations into conductivity changes, ranging from studies of malignant tumours to the fundamental processes of cellular death. His *Bipolar Theory of Living Processes* (1926) - based on the concept of the 'unit cell as a bipolar mechanism' - first brought to the attention of a broader public such fundamentals (to be topped off a decade later by *A Radio-electric Interpretation of Life*). 'Dr. Crile Suggests That Our Bodies Are Electric Batteries', as the *New York Times* reported in 1926. The notion deeply resonated with interwar bodily sensitivities, directly translating, in turn, into Crile's considerable public stature.[455] Crile's electro-energetic musings found a following not least among those 'nervous folk' suffering the shocks of modern life, and the accompanying, inevitable depletion of nervous energies.[456] The subject of electrical

451 Blood, and blood transfusion, were subjects deeply resonating with physical chemistry; on blood transfusion, see esp. Schneider (1997); Pelis (2001).
452 Crile (1915): p.3; p.37; Crile (1936): p.40; Crile (ed.) (1947): p.328.
453 Crile (1915): p.vii; Crile (ed.) (1947): p.328; pp.369-370.
454 Crile (1926): p.7.
455 de Kruif (1926): p.BR4; on these sensitivities, see esp. Thomas de la Peña (2003); also see Killen (2006).
456 Richter (1927): pp.7-10; p.85; also e.g. J.A. Jackson and Salisbury (1921); more generally, see Thomas de la Peña (2003); Lerner (2003); Killen (2006).

energies was one ‘packed with mystery and promise’ indeed: ‘the way seeds sprout, the way eggs hatch, the way radios function, and even the way we feel when we get up in the morning, the latest tests have shown’, as *Popular Science Monthly* informed in 1934, ‘are affected by flowing, invisible charges of electric power’, citing the ‘famous’ Crile: ‘Electricity keeps the flame of life burning in the cell.’[457]

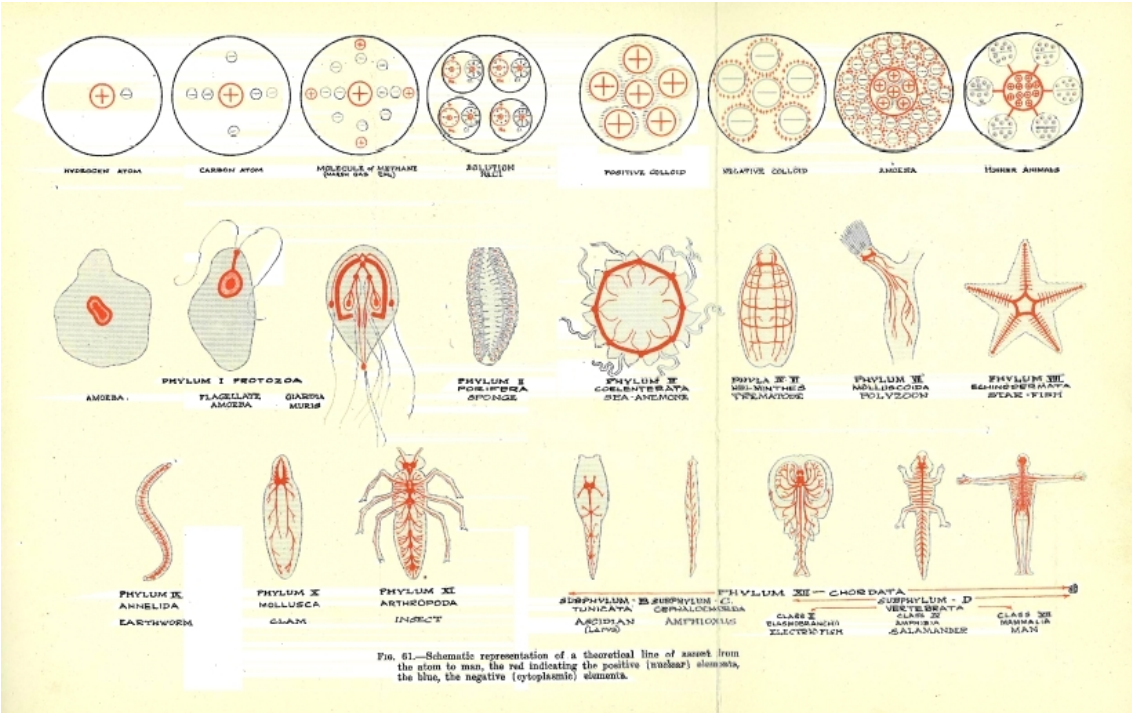

Figure 23: The 'bipolar' view on life, 1926

Predictably, Crile’s sweeping biophysical oeuvre failed to enlist much sympathies among the more academic students of living processes, who more likely were to sneer at ‘Crile’s rather loose and uncritical methods of work’. Biophysical effects, a measure of the pervasiveness of their technological substrates, clearly weren’t easily controllable then, neither practically nor discursively. Crile easily and routinely hit the news as for instance, when he ‘pictured’ ‘radiogens’ - infinitely small, protoplasmic ‘hot spots’ - in the protoplasm of man’s body in 1932, or when in the same year he recreated life - ‘autosynthetic cells’ - out of minced and dried animal brains.[458] But historically, the likes of Crile cannot be so easily dismissed;

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[457] Teale (1934).

[458] Osterhout to Harris, 13 June 1928, FRICKE/CSH, folder ‘Dr Hugo Fricke’ (folder 3/3) and Crile, Telkes, and Rowland (1932); nn. (1932b).

certainly not, at the expense, say, of events such as Nils Bohr's famous 'Light and Life' lecture, also in 1932, but far better known to historians of science.[459]

Even Bohr's lecture occurred in front of an *International Congress of Light Therapists*. The borderlands of physics and biomedicine were not primarily of intellectual vintage, as we already had ample time to see. The material intersections of circuitry, medico-physical borderlands and bioelectrical tinkering will be no exception. Like no few others of his frame, Crile's mind may have been an adventurous one, but by the same token, he was a true, hands-on biophysical enabler, no mere speculator. The Cleveland Clinic was one of the numerous venues which provided for many an investigator a first contact with, if not, a more permanent home in these borderlands.[460] From here, Otto Glasser, remembered mostly as a biographer of Roentgen, was pushing the case of *Medical Physics* (1944) and *The Science of Radiology* (1933); he had joined Crile's enterprise in 1922 (after quitting his previous job with the German *BASF* concern).[461] Meanwhile, Fricke's electro-technical expertise was enrolled in Crile's sprawling programme, and soon after, Kenneth Cole made it on the temporary staff list as well (more on which later). Fricke, the director, now developed his work in biophysics 'chiefly' along two lines as he later commended himself to the Cold Spring Harbor Laboratories: 'The biological effect of radiation and the electric polarization and conductivity of biological cells.' The former concerned such utterly practical problems as the 'physical foundation for practical x-ray therapy';[462] the techniques developed in conjunction with the latter, conductivity measurements at high frequencies, as will become clearer in due course, formed the basis of seminal investigations into the nature of the nerve impulse, beginning in the mid-1930s. But the origins of such

[459] The lecture was reprinted, among others, in Nature, see Bohr (1933); There has been a strong tendency to see interwar biophysical developments through the physical/philosophical lens of figures such as Bohr, Delbrueck, Schroedinger, Jordan, Slizard, etc see e.g. McKaughan (2005); Aaserud (2003); Kay (1985); Beyler (1996).

[460] To Crile we would have to add figures such as Ludolf von Krehl and Friedrich Dessauer in Germany, Leonard Hill in the UK, Alexander Gurwitsch in Russia, Pierre Lecomte du Noüy in France, Wilder Bancroft in the US, or William Bate Hardy, Frederick Donnan, and Alfred Loomis (some of whom we have indeed already met.)

[461] On Glasser, see L.S. Taylor (1965).

[462] Fricke to Harris, 31 July 1928, FRICKE/CSH, folder 'Dr Hugo Fricke' (folder 3/3)

experimental systems resided elsewhere: in places like Cleveland, Ohio.

There, Fricke had begun to pursue high-frequency measurements with such items as blood suspensions, bacteria and various animal tissues. And here we begin to approach the world of circuit-equivalence: High-frequency resistance measurement was a 'precision method' which had, its theoretical interest apart, certain 'practical implications' as well.[463] In a 1926 paper on 'The electric capacity of tumors of the breast' Fricke thus explained how a suspension of biological tissue when inserted into an electric circuit could be revealed by such means as 'behav[ing] as though it were a pure resistance in parallel with a pure capacity'. If this provided a rough picture as to what was going on in such suspensions (tumours provided a 'most convenient and uncomplicated material for study'), it also turned out that 'certain types of malignant tumors' had abnormally high such capacity. There was, not only on Fricke's mind, tremendous diagnostic potential to such high-capacity behaviour.[464] Moreover, as attentive readers of Crile's *Bipolar Theory* would have known, in investigations such as this, 'Dr. Fricke ha[d] found that the film which surrounds ... [biological] cells is in the order of 4/10,000,000 of a centimeter thick'. Such 'films of infinite thinness', according to Crile, were 'peculiarly adapted to the storage and adaptive discharge of electric energy'. Their nature, accordingly, was of immense interest.[465]

Fricke's high-frequency forays into the electric nature of biological membranes, meanwhile, occurred at a time when the more business-minded men enthused how thanks to short-wave radio-broadcasts, these 'once useless very short waves [were] becom[ing] most valuable'.[466] Fricke, in turn, was no original mind. 'Earlier investigations were handicapped', as Fricke surmised in 1933, 'by the experimental difficulties of producing alternating currents over a wide range of frequencies. This difficulty was overcome by the introduction of the audion oscillator, which initiated a period of considerable progress.'[467]

463 Ibid.
464 Fricke and Morse (1926): p.340.
465 Crile (1926): p.15.
466 nn. (1931a).
467 Fricke (1933): p.117.

'An interesting application' of such measurements, as Fricke knew well enough - because it had been done before (albeit with limited success) and because it was being done, as we shall see shortly, in many places elsewhere - indeed consisted in the calculation of membrane *thickness* (on which these capacities depended). More generally, variations in tissue resistance when subjected to alternating currents of varying frequency allowed inferring from such changes in *impedance* the physical properties of the biological objects so investigated.

Accordingly, the mobilization of high-frequency currents for biological purposes was not confined to what in effect was taking shape here, with hindsight, as a significant route to the elusive nature of the nerve membrane. The latter, evidently, merely formed part of a broad spectrum of interesting objects. Fricke himself was particularly fond of suspensions of red blood cells, bacteria or tumours, a series he supplemented with a range of other simple model-substances - milk, cream, or gelatine - whose fat-content (another useful application) was easily determined by way of conductivity measurements.[468] Such investigations Fricke proposed to continue, with the 'marine material which can be procured at Cold Spring Harbor' once the plans for his re-location took shape during 1928.[469] 'It [was], of course, well known', he assured his future employers, 'that electrical changes usually follow life processes'.[470]

During the next two decades and due, not least, to Fricke's ambitions, the Cold Spring Harbor laboratories would famously turn into a seedbed of academic biophysics.[471] But still, and more importantly here, like many of his peers, Fricke inhabited less-than-stratified biophysical borderlands, learning and pursuing their trade in environments such as Crile's Cleveland enterprise where one moved easily from x-rays to excitable tissues to artificial cells and back again. Cole above, as we shall see, was one of them. These cases, in

[468] Fricke to Harris, 31 July 1928, FRICKE/CSH, folder 'Dr Hugo Fricke' (folder 3/3)

[469] Fricke (1925): p.137 and Fricke to Harris, 31 July 1928, FRICKE/CSH, folder 'Dr Hugo Fricke' (folder 3/3).

[470] Memorandum 'Dear Gentlemen...', (1930), FRICKE/CSH, folder 'Dr Hugo Fricke' (folder 3/3)

[471] See E.L. Watson and J.D. Watson (1991): chapter 3.

turn, we should not construe as those of physicists colonizing biological science. Rather, as we shall see in the following, these hogde-podge ventures in medical physics and the eclectic, makeshift technical cultures of biophysical science they sustained, were themselves an expression of their electrified, pervasive technological substrates.

Materially, what is called medical physics here was by all means a bizarre assortment of electrical instruments and physical gadgetry. So much so, in fact, as to prompt regulatory measures, as happened, for example, in 1930 when the British Medical Association installed a Register of Biophysical Assistants.[472] It stretched from quartz-lamps for home use to (increasingly) off-the-shelf devices for purposes as diverse as electrocardiography, x-ray, or myotherapy with which the world was flooded by firms small and large: Radionta, Siemens, Hewittic Electric Co., the British Hanovia Quartz Lamp Co., GEC, Icalite, Ulvira, Cox-Cavendish Electrical, The Medical Supply Association, Watson and Son Electro-Medical Ltd, and many more. It was not least this sprawling electro-technological infrastructure that gave reality to a host of biophysical effects, and as such it was enmeshed with a similarly eclectic, peculiar form of 'technical identity': Identities such as Fricke's, I shall argue, had a semblance with the technical hobbyist first, and the professional engineer only second.[473] This consideration will be an important one in terms of how we conceive of electro-technology mediating the biological imagination; and even more important here, of how we conceive of modeling practices and circuitry not merely on the level of metaphor, and neither as expressions of local knowledge, but as practically anchored in broader historical circumstances. This will become clearer now as we move beyond Fricke and turn in broader terms to the *bricoleur* dimensions of interwar bioelectrical tinkering.

[472] nn. (1930b).
[473] On this notion of technical culture, see Haring (2006): esp. pp.1-7.

The electronic arts

The *bricoleur* here, of course, is an allusion to the incorporations of Lévi-Strauss's anthropology of the *Savage Mind* into studies of the scientific laboratory. As someone having as his object a 'science of the concrete' achieved by 'devious means', Lévi-Strauss's characterization of this bricoleur (as opposed to the 'specialist' or 'engineer') is certainly an apt one here as well. [474] The following, however, is less strictly concerned with this anthropological abstraction than the specific historical resonances of the non-disciplined, biophysical bricoleur and the contemporary, technical cultures of wireless. For our purposes, it is more illuminating to simply stick to a literal, and historically grounded, reading of such scientific *tinkering*. For, the correlate of the labile social and institutional structures of interwar biophysics was a very literal form of such tinkering - a historically specific economy of instrumentation and experimentation. It intersected and reflected the material and conceptual cultures of radio-technology of the day. And it was central to the way electro-technical and biological knowledge were mediated.

In the period between the wars, bioelectrical model-makers weren't made, or schooled, or formally disciplined and locally instilled; rather, like the bricoleur, they emerged in the midst of things. While a training in practical physics clearly would have been 'ideal for [this] sort of work', as Detlev Bronk, director of the Johnson Foundation for Medical Physics mused, it posed the vexing problem of 'recruits'.[475] The 'ideal' case, the man trained in both physics and biology, he once informed a Rockefeller Officer, was 'asking [for] too much'.[476] The relevant skills, fortunately, were by and large out there. And they tended to enter bioelectrical practices along indirect routes. Much acclaimed, for instance, Cambridge physiologist Bryan Matthews, excelled, as a former radio-hobbyist, at the design of instrumentation; the same autodidactic virtuoso talents distinguished the

[474] Lévi-Strauss (1966): esp. pp.16-17.
[475] Bronk to Randall, 27 June 1930, RF/RG.303, Box 82, Folder 6
[476] See 'list of possible recruits'; Bronk to Gregg, 16 July 1929, RF/RG.303, Box 82, Folder 6

future biomedical engineer Otto Schmitt - brother of the more famous pioneer of 'neuroscience' Francis Schmitt - who enlisted, barely out of high-school, in A.V. Hill's 'program [of] studying nerve and muscle quantitatively' in 1937.[477]

Such cases were far from atypical. But more broadly and profoundly, it was the transformation of interwar life-worlds, driven by the burgeoning radio-electrical industries that began to shape, perceptibly, if often indirectly, the face of electro-biology. Telephones, radio, electrical lighting and other gadgetry then turned from exotica into items of everyday use, and as historians of technology have argued, not only did there emerge lively, non-specialist cultures of radio-tinkering, electrical media reformatted interwar sensoria and sensibilities, quite generally. Rudimentary television, photocells and similar such electro-optical wonders ushered discourses of *electric eyes*, while radio and electro-acoustic technologies changed the social experience and meanings of *sound*.[478] It was not long until new and fleeting, aural spaces of experimentation and demonstration were supplementing the inscriptions of bioelectrical phenomena into visual media; they formed part of the broader interwar transformations in sound technology and practices of listening. Students and physiologists were able to experience the 'firing' of neurons immediately and thus more intimately, as part of a shared, social auditory experience that must have resembled the gatherings around home radio-sets.[479]

Making 'audible heart sounds via radio-broadcast through all of Europe' was now merely a question of doing it. Telephones, phonograph records and loud-speakers then entered the technical armature of physiologists definitely, converting their ostensibly graphic method into a more multi-sensory experience ... 'rat-tat-tat-tat', so the 'sound' of nerve messages.[480] Most suitable for class-room use, sound technologies were easier tamed

[477] Gray (1990): p.275; Schmitt (1990): pp.114-116; Harkness (2002): pp.467-469.

[478] E.g. Abramson (1995); Thompson (2002); Andriopoulos and Dotzler (eds.) (2002); Wurtzler (2007).

[479] Lythgoe (1934); for an authorative survey of available sound technologies and physiological applications, see Scheminzky (1931).

[480] E.g. Durig, 'Bericht über das Habitilationsgesuch', June 1927, SCHEMINZKY; and see Folder 'Bronk lectures, 1926-1941', RF/RG.303, Box 14, Folder 1; and press clipping, Herald Tribune, 28 December 1934 (copy in Box 62, folder 2)

than the still fickle electronic techniques of visual display. '[A]uditory observation to a trained ear can give almost as much qualitative information of activity in a nerve as an oscillosgraph record, and this qualitative analysis can be made instantly, while analysis of the record requires much time.'[481] Electricity, oscillations, and all manner of waves and radiation were omnipresent, continually but imperceptibly interacting with the living, though few people understood even the rudiments of such phenomena: 'If we go into a field anywhere in England at this moment, wireless waves are whistling around us from all directions, but unless we have a portable receiver with us we know nothing about them, and cannot show that they are there. In the same way, to appreciate the currents of our bodies we must convert them into something that can affect our senses.' The year is 1931, we listen to a *BBC* broadcast on the *Electricity in our Bodies*: '[V]ery sensitive detecting system[s]' were required to display these subtle spectacles of nature, the above Matthews here explained. And who knew that 'almost identical sounds' were produced by the currents recorded from a human muscle (Matthew's muscle) and a 'killed frog's leg'? Such 'commonplace[s] in physiology' were now most effectively demonstrated – transmitted - to radio listeners sitting in front of their home-sets.[482]

Traversing these realms were experiences such as that of 'noise'. 'Noise in amplifiers', as the *Bell System Technical Journal* reported in 1935, 'is now a familiar term': '[A]ny one who has had his favorite radio hour ruined by static noise' had some experience with it, or with the noise induced through 'poor batteries, loose contacts, gassy tubes'.[483] The problem thus was, in the first instance, a practical and *familiar* one, one of keeping a continual, watchful eye on the performance of one's set-up, one of tuning, tinkering, and adjusting. This set of techno-cultural skills did not belong to either the laboratory, the workshop, or one's garage exclusively. Noise, its actual or potential presence, increased the

481 B.M.C Matthews (1935): p.212.
482 B.M.C Matthews (1931): pp.5-9; pp.27-30.
483 J.B. Johnson and Llewellyn (1935): p.85.

demands on experimental skills, and permanently threatened to distort one's *signals*: a nuisance to radio hobbyists and experimenters alike.[484]

Instrumental appropriation and creative re-use characterized the experimental culture at hand. The first uses of the telephone in physiology, as a *Muskeltelephon*, in fact dates back to the 1880s, but the systematic use of such components had to await the broad-scale commodification of electrical products after WWI. The vacuum tube, and wireless technology generally, then turned from experimental into commercial products. By 1923, 4,500,000 tubes were produced annually in the US, a figure reaching 69,000,000 in 1929, prices for tubes and materials plummeting. '[K]aleidoscopic changes', *Electronics* recorded, were underway in the electrical industry.[485] Wave-lengths diminished ever more rapidly, and the confusing complexity of this electrical world - a true zoo of diodes, triodes, tetrodes, pentodes, thyratrons, magnetrons, rectifiers and oscillators - soon was reducible, it seems, only by taking recourse to the organic metaphoric of *evolution* and *family trees*.

[484] J.B. Johnson and Llewellyn (1935); Adrian (1928): pp.37-42.
[485] See editorial, nn. (1930c): p.366.

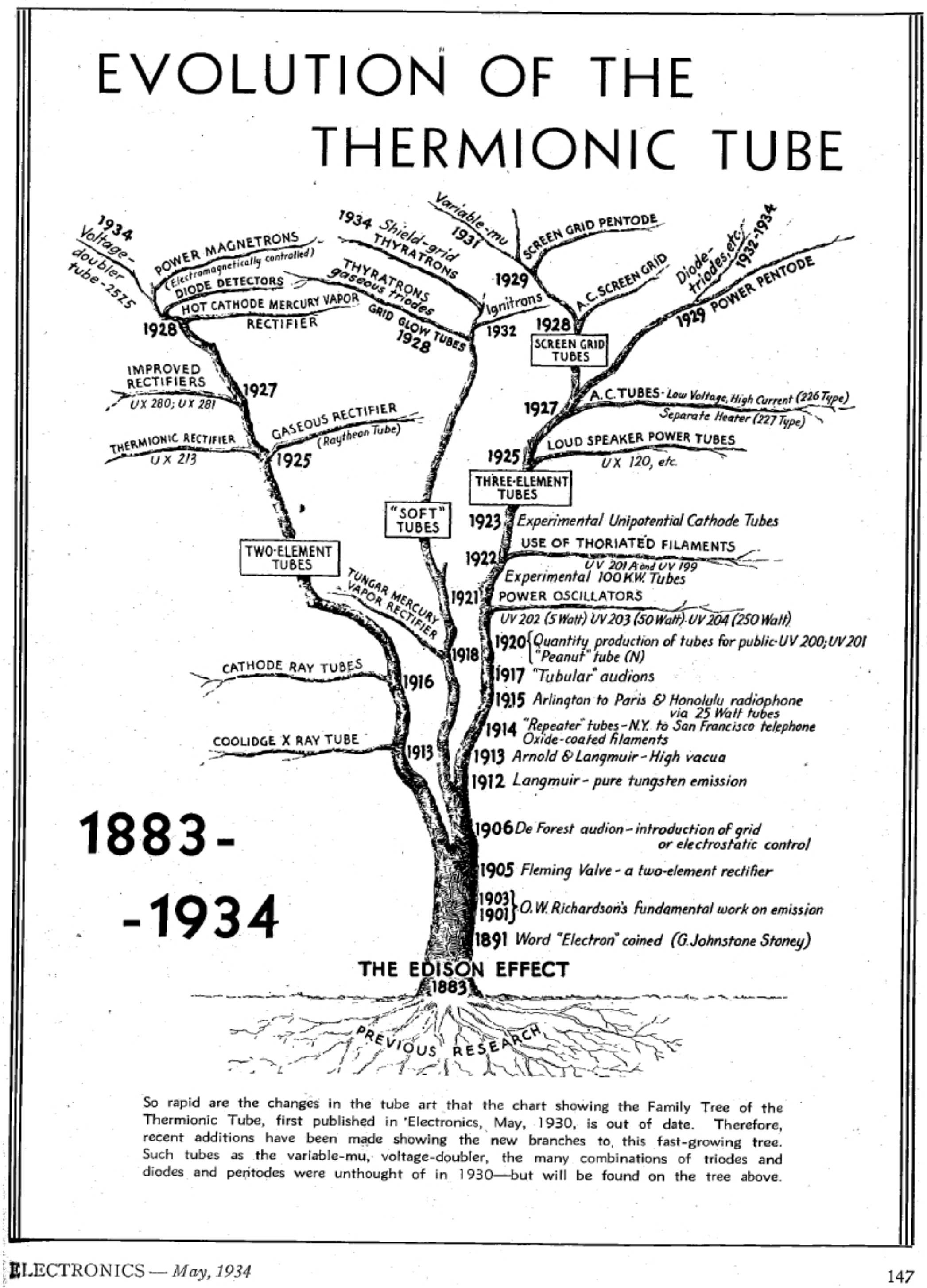

Figure 24: technological evolution, 1934

Despite the frequent rhetoric of 'revolution', as already noted, the inroads of 'the electronic arts' into physiology were protracted, however, and far from even.[486] If electrical

[486] Frank (1994); Borck (2006).

progress called up a natural history of devices, the devices themselves were of a beastly kind. Early amplifier set-ups and cathode ray tubes suffered from a great variety of problems, often prompting physiologists to take recourse to less rapid, mechanical inscription devices. The 'common faults of cathode ray tubes have been short life, non-uniformity, poor control of brilliance', as *Electronics* reported in 1933. They had been 'awkward'. Especially non-recurrent, 'transient electrical phenomena' proved a problematic object.[487]

The nerve impulse was one such transient phenomena. Developers and users of devices when voicing such complaints usually had in mind lightning surges which haunted power lines or signals in telephone networks that failed to appear sufficiently clearly on their oscilloscope screens. But whatever the exact object, it was basically 'impossible to view the curves on the screen ... because the trace produced by a single sweep of light sport across the screen is insufficient to make an impression on the eye and furthermore there would be no time for a detailed study of the curves.'[488] As one compromise, physiological early adopters tended to turn to oscillatory, repetitive phenomena rather than singular events: Then, forfeiting the singular impulse, 'the spot of light, which reveals the course of the action current trace[d] its curve repeatedly over the fluorescent screen.'[489] Over the years, improved, faster and brighter screen materials, stabilized tubes, and more focused, concentrated beams by and large removed such misbehaviour.[490] 'You will find the C.R. tube a joy to use', one biophysicist wrote in 1936, almost unbelievingly.[491]

And still: there never was a notion here of simply *using* an instrument. This may sound trivial, given, not least, that this is what historians of science now tend to assume,

487 C.W. Taylor, Headrick, and Orth (1933).
488 H.M. Turner (1931): p.268; Adrian (1928): p.43.
489 Forbes, Davis, and Emerson (1931): p.2.
490 Rogowski, Flegler, and Buss (1930); Ardenne (1933): esp. preface ; J.L. Miller and J.E.L. Robinson (1935); Stinchfield (1935); Ardenne (1960); for a technical history, see P.A. Keller (1992).
491 Pumphrey to Bronk, 16 April 1936, RF/RG.303, Box 52, Folder 19; and see B.M.C Matthews (1935).

generically. But it is not quite as trivial as that. Partly, because we can and should understand *usage* more historically; and, partly too, because in the present case, to exaggerate only slightly, there were no *instruments*. There were 'set-ups', 'outfits', and increasingly so, 'systems' - wired and plugged together from a vast choice of components. Despite the tendencies towards *commodification* (which went along with a broad-scale *deskilling* of the radio-consumer), the art of bioelectrical measurement technologies remained in a state of relative openness and fragmentation.[492] Unlike the cases that dominate the historiography and arguably, our thinking about instruments – *compact, black-boxed objects* such as the ultracentrifuge or the electron microscope - the component-based recording *systems* so dear to electro-physiologists largely resisted objectification.[493] They remained relatively loose and local assemblages, and it wasn't until the late 1950s that a new breed of 'biomedical engineers' would begin to impose definite levels of standardization and homogenization.[494]

The circulation of an increasing range of special purpose circuits, 'accessories' and *Kunstgriffe* betrayed this inherence of *use-as-tinkering*. And still in late 1930s, as biophysicist Bronk complained to the editor of the *Review of Scientific Instruments,* things, sources, and the literature, were 'badly scattered' indeed.[495] In the same year, 1936, the first textbook devoted to bioelectrical *Messtechnik* appeared - in German. Filling a 'precarious gap', its author, Wolfgang Holzer, an assistant at the physiological institute in Vienna, now supplied an exhaustive overview of this unfortunately most 'dispersed' subject.[496]

As much as such efforts reflected moves towards normalization and homogenization, they reflected an existing technical culture based on self-help, personal

492 See Butsch (1984); Wurtzler (2007); Alcorn (2009).
493 The extent to which next-to-universally employed instruments such as the cathode ray tube have failed to generate much historical interest is one indication of this; two noteworthy exceptions are Hessenbruch (2000); Hughes (1998).
494 E.g. Schwan (1991).
495 Bronk to Richtmyer, 22 October 1936; Richtmyer to Bronk, 27 October 1936; RF/RG.303, Box 52, Folder 35
496 Holzer (1936): p.VIII.

contacts, and the eclectic appropriation of skills, knowledge and electrical things. If *using* electrical apparatus was *bricolage,* it was so in historical terms – because it resided, as it were, in the nature of interwar electrical things, and because one still was dealing, by and large, with what one called the *electronic arts*, not yet, with *electronics*, the science. Now obscure figures such as Holzer, Fricke, or the Viennese physiologist Ferdinand Scheminzky were bioelectrical tinkerers in exactly this sense. Scheminzky's far-ranging engagement with the world of bioelectrical phenomena indeed usefully captures the improvisatory biophysical identity that is at issue here. Like few other contemporary biological scientists, Scheminzky laboured the case of the electronic arts, drawing together the pertinent literature, tricks of the trade, applications and recommendations. But other than that, Ferdinand Scheminzky was truly unremarkable.

The son of an Austrian railway *Beamter*, Scheminzky produced at a fact pace and, quite typically, on a great many subjects: practical laboratory manuals, electro-acoustics, bioelectricity, and later in life, the radium and ions in the healthy waters of the alpine spa Bad Gastein all belonged to the portfolio.[497] Pervading Scheminzky's oeuvre, naturally, was the universal vacuum tube. Initiated to the device by one of its many inventors, the Austrian telephone-engineer Siegmund Strauss, around 1920, Scheminzky had set out to chart the manifold possibilities of the electron-tube: The 'permanent electrical perfusion on fish', 'differential sensitivity of trout eggs', 'electrotaxis', 'oscillotaxis', and 'electronarcosis' so came under Scheminzky's electro-technical purview – always with an eye on practical results: '[F]isheries in Germany', as Arnold Durig, head of the Vienna Institute proudly noted by 1927, 'already attempt[ed] to exploit the method [of electronarcosis] for commercial fishing'. A pedagogical innovator, Scheminzky broadcast bioelectrical phenomena through lecture theatres and over the radio, and more impressive even was Scheminzky's 1928 contribution to Abderhalden's *Handbuch der Biologischen*

[497] See Auerswald (1975).

Arbeitsmethoden. A survey of the applications of the electron-tube in biology, it expounded the 'state of the art' on more than 300 pages. It was to-date 'unique' as a source for the biologist as regards this 'modern' *Technik*.[498] Scheminzky's outpourings did, of course, broadly keep with the genre of handbook and scientific article; they were employing too, however, registers more familiar from the radio-amateur and DIY-type literature.

This was due, not least, to the nature of the subject. Scheminzky thus routinely deferred to such 'valuable' 'details' as could be found, for instance, in Banneitz' *Pocketbook of Wireless Telegraphy and Telephony* (1927), or the 'well-known radio magazine' *The Wireless World*.[499] The 'universal' character of the electron tube was Scheminzky's message, but the more mundane dimensions, precautions to be taken when connecting electrical appliances to the commercial power supply (haunted by frequent 'disturbances') found consideration as much as the tricks to prevent nerve-preparations from being 'short-circuited'. The bewildering range of applications was matched only by the still more bewildering variety and choice of components, devices, parts - and their combinations. Readers were guided to circuits of established utility, and pointed out the best available brands of neon-lamps (widely used for 'Reklamezwecke' [advertisement purposes] and most suitable for the purposes of rhythmic stimulation), telephone-condensers, switches, gramophones, and, of course, vacuum tubes. Scheminzky generally made it a point to navigate the potential user through the world of electro-technical consumerism: high quality usually had to be insisted on.[500]

This, the style of Scheminzky's outpourings, was characteristic of much biophysical writing in the period. The ardent reader of the pertinent literature not least encountered a plethora of 'tricks' or *Kunstgriffe*. Without a *Kunstgriff* it often would have been impossible to 'eliminate' the manifold distortions that haunted the bioelectrical experimenter.[501]

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498 Durig, 'Bericht über das Habitilationsgesuch', June 1927, SCHEMINZKY; and see Scheminzky (1926); Scheminzky (1928); Scheminzky (1931); Scheminzky (1932).
499 Scheminzky (1931): p.707; p.734.
500 Scheminzky (1926): pp.126-127.
501 Ebbecke (1917); Ettisch and Péterfi (1925); Trendelenburg (1931); Lullies (1931); Holzer (1940).

Likewise, it was mandatory to 'simplify the reconstruction [Nachbau]' of the designs employed; not so much for the strategic sake of *reproducibility* but because the moral economy of tinkering demanded so. [502] Fortunately enough, 'handy, lucid, and comfortable' apparatus was easily assembled by making exclusive use of components 'as being used in radio technics and now being available everywhere, at relatively low cost and in excellent finish.'[503]

From tinkering to modeling

Cases such as Scheminzky's are important in so far as they reveal a technical world of bioelectricity that would largely be lost were one to approach from the narrow, disciplinary perspectives of nerve physiology and the results, merely, of *research.* It were the Scheminzkys, Frickes, Glassers, and Criles who kept going the circulation of practical knowledge, of biophysical effects, and of electrical things. Rather than, that is, the Adrians, Erlangers, or even Hills. And all this perhaps would not be all that remarkable were it not also the case that the diffuse networks within which bioelectrical *Messtechniken* took shape - somewhere between bioelectrical bricolage and medical physics – a particular form of biological knowing was generated. They were the ones which produced *models* – real circuitry – rather than, for instance, chasing the 'laws' of excitation: *laws* – systematic relationships between stimulus and recorded response - were something much dearer to the heart of the academic nerve physiologist.[504]

To begin to see this, take Wolfgang Holzer, a sometimes colleague of Scheminzky's, and the already mentioned author of a 1936 treatise on bioelectrical *Messtechnik*. Holzer – a

[502] Holzer (1940): p.222.
[503] Heller (1930): pp.195-196; also see J.G. McKinley and G.M. McKinley (1930); B.M.C Matthews (1935): p.510.
[504] on this preoccupation with laws, see esp. Davis and Forbes (1936): p.407; p.410; also see Cremer (1929); Cremer (1932); Schaefer (1934a); Lapicque (1935); A.V. Hill (1936); Rashevsky (1938).

trained engineer - too was a true bioelectrical *bricoleur*, ranging widely through the world of biophysical phenomena and all the while he was busy collecting tricks, modifying, advising, tinkering and adapting his more professional knowledge to the special requirements of measuring vital processes. Having shared his training at the *Institute for High-Voltage Technology*, Berlin (an acclaimed centre of cathode ray tube development and research) with two future pioneers of electron-microscopy - Dénis Gábor and Ernst Ruska [505] - Holzer thus just recently had come out with the *Foundations of Short-Wave Therapy: Physics-Technics-Indications* (1935). Holzer spoke with some authority in these regards, already having established a track-record of contributions concerning such diverse items as electrical fish-traps, action currents (*Aktionsstromforschung)*, and certain *Modelltheorien* of current-density distributions in living materials.[506] And here Holzer, of course, too drew on the tremendous amount of practical, electro-cultural knowledge that was both, local and everywhere.

At the time, Berlin, like Vienna, like London, and like any other electrified city was traversed by an impressive range of lose connections between physiologists, clinicians, firms, workshops, and electrical engineers - a collective, if scattered knowledge regarding bioelectrical *Messtechnik*. Holzer's own circles included such figures as Manfred von Ardenne, engineer-entrepreneur, busily proselytizing about the art of amplification or 'advances in television' but always eager to show 'how, through collaboration in the borderlands between physics and medicine, interesting possibilities [could] be opened up'.[507] They also included Hans Rosenberg, originated from the Physiological Institute of the Veterinary School, and another pioneer - in cooperation with the Siemens-Wernerwerke – of the art of thermionic amplification;[508] or again, they included Gábor who, while in Berlin, himself delved into a cooperation with the physician Reiter – the result being

[505] The best historical sources on cathode ray tubes tend to be histories of television; for a more technical account, see P.A. Keller (1992); on the early history of the electronmicrosope, see Rasmussen (1997a): chapter 1; on Gabor, see Johnston (2006).
[506] Esp. Holzer (1933): pp.822-824.
[507] Werner and Ardenne (1931): pp.257-258; and see Ardenne (1938).
[508] Hill to Bronk, 4 February 1935, RF/RG.303, Series 303-34, Box 87, Folder 16; on Rosenberg, see nn. (1963b).

several *Siemenskonzern Sonderhefte* - on the somewhat dubious subject of *mitogenetic rays* and their detection.[509]

Clearly, seen from the chaotic ground up, not the cash-flows and streamlined programmes triggered by the Rockefeller Foundation, a form of adventurous dilettantism was programmatic to this biophysical science and its borderlands. What is less clearly perceptible is that as such, it was utterly productive. There was, to be sure, essentially little *really* new here, no revolutionary discoveries, nothing the odd nineteenth century (bio)electrician wouldn't already at least have gestured at. As Justina Wilson, head of the Electrotherapeutic Department of the Royal Free Hospital, London, pointed it out, Holzer's *Foundations* above provided a competent 'summary of the physical and electrical principles' involved in 'the action of ultra-high frequency currents on biological materials'.[510] Holzer there had delved deeply - and in very technical fashion - into some fundamental considerations concerning some biological quantities 'of the highest importance'. They sounded fairly unspectacular and familiar: resistance, dielectric constant, and polarisation capacity.[511]

But the impression is not entirely correct. As theoretical entities, or for the purposes of calibration, quantities such as (tissue) resistance had long interested physiologists, but ultimately, their projects – predicated on regimes of stimulation/response/inscription - were geared towards other ends and constructs – many of them soon to be derided as merely 'phenomenological' 'laws' - treacherous correlations: constructs such as the *time-to-excite*, for example or most infamously perhaps, the so-called *chronaxie*. In contrast, for Holzer those quantities turned central which, or so one said, had real 'physical sense'.[512]

The likes of Holzer *measured*. And not least for practical purposes, this required

509 See esp. Reiter and Gabor (1928).
510 Holzer and Weissenberg (1935): pp.7-8.
511 Ibid., esp. pp. 73-81.
512 Achelis (1933): p.233; Rushton (1934): p.483; Schaefer (1934b): p.165; more generally, see esp. Joy Harvey (1994).

models. Indeed, like many a like-minded student of vital phenomena - and they had become legion – Holzer worked preferably with model-objects, and especially so, simple ones: trout eggs or micro-organisms, for example. Suspended in a high-frequency electrical field, or what he called 'the irritation space' - *Reizraum* - they were easily pictured as 'volume[s] of high conductivity, briefly called', as he said, 'the 'body' here'.[513] There was no coincidence here. Given the nature of his job, Holzer worried especially about ways to control the flow of currents through a (human) body - a problem encountered, prominently, in high-frequency therapy. Accordingly (and we will encounter many more examples), the kind of model Holzer was interested in targeted the spatio-temporal and physical 'conditions' that a biological object was manifesting in a *Reizraum*: its electrical properties, and their variations as the *Reizraum* underwent changes. For very practical reasons, then, Holzer wasn't much interested in grand theory or *law*-like phenomena for their own sake. His models were to be *used*. And thus, however simple, they were to manifest physical sense.

In itself, there was nothing particularly revolutionary here. But, as we shall see, such fairly technical practices - and high-frequency technologies especially - *did* make a difference to what bioelectricity *was* and how it was approached. The real difference resides in scale: Epistemologically we are talking not about novelty and certainly not about excellence but common staples. Quantities rather than qualities: a bioelectrical *World-picture* that rather than particular (electrical) pictures. If the latter had been floating around for decades, innumerable bricoleurs now gradually but persistently worked them into a technical, materially and practically grounded vision of life. This is why they deserve a prominent place in this story. This world-picture, as the following section shows, was in fact fairly concrete. And as such, it had everything to do with real circuitry.

513 Holzer (1933): , pp.822-824.

Circuitry and circuit thinking

The interwar student of the cell, his going about his business, was entangled in manifold ways in the technological life-world of the day. Hence the emphasis on elements of contemporaneity, rather than genealogies and precursors. A similar ethos, and certain forms of bricolage, would seem familiar of course from academic, 'string and sealing-wax' physics and even nineteenth century physiology. But like the latter, experimental physics too was a tradition which then was deeply inflected, as Jeff Hughes has argued, by the diffusion of electro-technological skills and more broadly, by 'radio-culture'.[514] And in its details and in terms of the cultural experiences that shaped them, these forms of biophysical tinkering resembled, significantly, more closely the burgeoning radio-amateur movement than, say, the organic physics of a Helmholtz or Du Bois-Reymond.[515] With the former, these biophysicists shared, not least, a material world of technological consumption. The idea, in turn, that electronics was primarily an *arts* was a widely accepted notion, the corresponding ethos not alien even to the (professional) radio 'set designer'. Traversing these domains thus were not only specific ways of dealing with apparatus, but ways knowing them as well. For, as *Electronics* noted in 1931, a 'radio set can be no better than its weakest part':

> 'The greatest genius', said Carlyle, 'is he who adapts and combines the best ideas of the greatest number.' And the best radio designer, the sage might have added, is the one who draws on and skilfully assembles the existing experiences of the best makes of components and parts.[516]

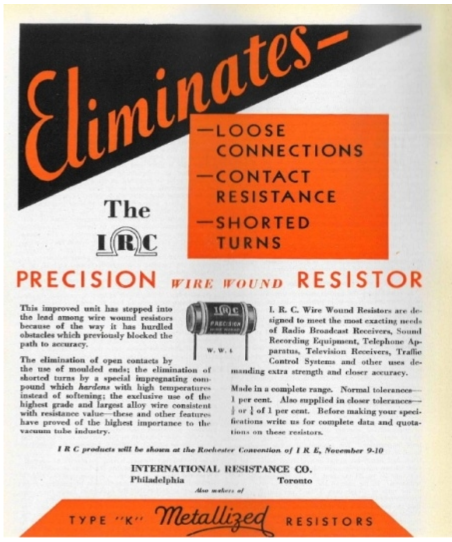
Adapting, combining, assembling. As historians, we don't have to read electric *bricolage* into the story. This world of electrical things, parts, and systems was being articulated as such by

[514] Hughes (1998).
[515] Esp. Haring (2006); also see Clarricoats (1967); D.E. Nye (1990): esp. p.280.
[516] See editorial, nn. (1931b).

the actors. The intimate association of genius, components, and parts could hardly have escaped even the cursory reader of journals devoted to the 'electronic and radio arts'. *Electronics* above, for instance, hitting the market in 1930, was promptly subscribed to by the Cambridge Physiology Department or the Philadelphia-based Johnson Foundation for Medical Physics.[517] 'A camp-fire for counsel', as its first editorial read, its pages were littered with advertisements promising 'control', 'precision' and 'modern methods' through superior component parts.

Figure 25: advertising precision. (Electronics, December 1931)

Figure 26: advertising precision. (Electronics, December 1931)



Such was the 'path to accuracy', and still more salient was the accompanying, visual language of electrical circuitry that pervaded the technical and popular scientific literature of the time. It routinely featured in biophysical publications as well. As experimental set-ups grew increasingly *systemic*, rarely would an experiment be reported without its detailed description rendered in the language of wiring diagrams.

[517] See *Electronics* to Bronk, 7 May 1930, RF/RG.303, Box 87, Folder 1; and note 'missing journals to locate', Box 82, Folder 5

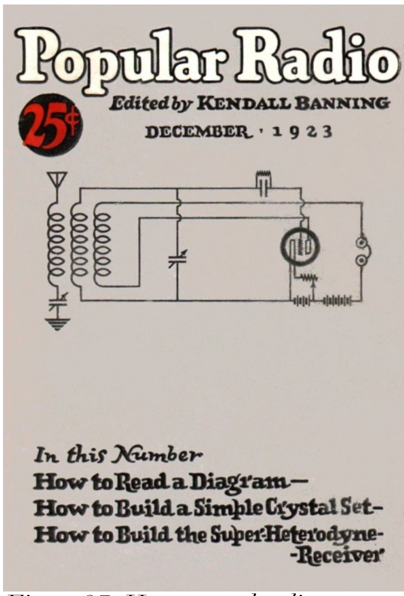
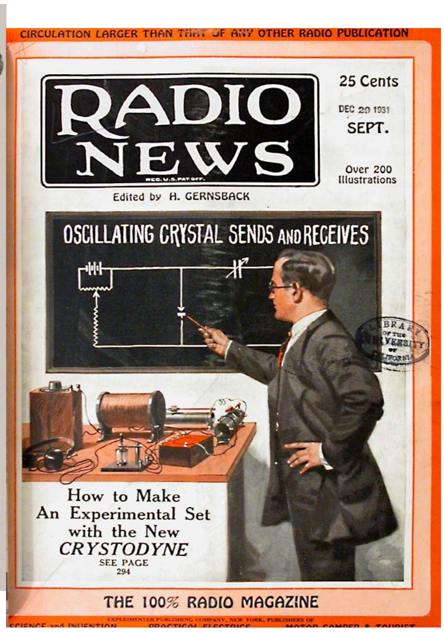


Figure 27: How to read a diagram: cover title, Popular Radio, December 1923

Figure 28: cover title, Radio News, September 1924



Even a text targeting a broad audience, such the already mentioned broadcast *Electricity in our Bodies* (1931) by Cambridge physiologist Matthews casually supplied (in the print version) detailed, 'technical descriptions' of set-ups, confidently assuming the requisite literacy on part of reader: 'most of us', it claimed, after all 'ha[d] some idea of the working of wireless, automatic telephones, and electric light'.[518] Historian of technology Wurtzler has spoken of this proliferation of circuitry in the period as *consumer pedagogies*, a term that usefully captures the kind of less-than-esoteric knowledge at issue here.[519] Like never before (and never after), was this visual culture of circuits, and the circuits themselves, exposed and grounded in everyday experience. The subtle impact of this familiarity is palpable in the sketches physiologists supplied of their 'systems'. Would, at the beginning of the century, the reader still have encountered an undisciplined *sketch*, almost organic in its appearance, by 1930, he or she was faced with an exacting, technical drawing:

518 B.M.C Matthews (1931): p.11; p.35.

519 Wurtzler (2007): chapter 2.

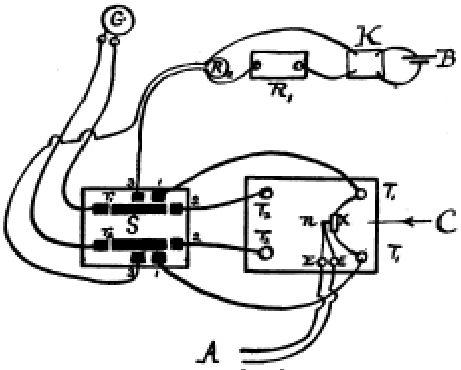


Figure 29: sketch, 1912

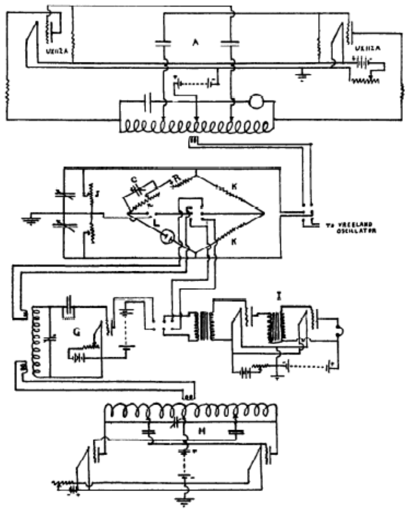


Figure 30: sketch, 1929

The sketch on the left, one might say, is anatomical in nature, a geographical map, representing a spatial lay-out: localized elements connected through wires running through space; its visual language owes more to the telegraph engineer's static map of a wired, electrified region or city than to the functional, diagrammatic machine drawings of the time. The drawing on the right, in contrast, though still map-like, lost its indexical relations to concrete elements of space.[520]

To the trained eye, it depicted the functionalities of a system rather than merely its spatial configuration. It was expressed, moreover, in an increasingly standardized visual language whose uniformisation paralleled the expansion of the profession of electrical engineering. Teachers then first perceived the need for 'drafting guides' in matters of circuit diagrams.[521] In major textbooks such as Johnson's *Transmission Circuits for Telephonic Communication: Methods of Analysis and Design* (1924) and Shea's *Transmission Networks and Wave Filters* (1929) (both issuing from the influential *Bell Labs*), circuit diagrams turned into devices of *design* and *analysis*: replete with rules of transformation and charts depicting such 'physically interchangeable equivalent networks'.

[520] In the post-war II period, such indexicality would disappear even further, on this see Jones-Imhotep (2008); also of interest, though lacking an analytical focus is Mellanby (1957); more generally, see Bennett (1993); Dunsheath (1962).

[521] Turner to Chaffee, 10 November 1932, CHAFFEE, Box 2, Folder 'T'

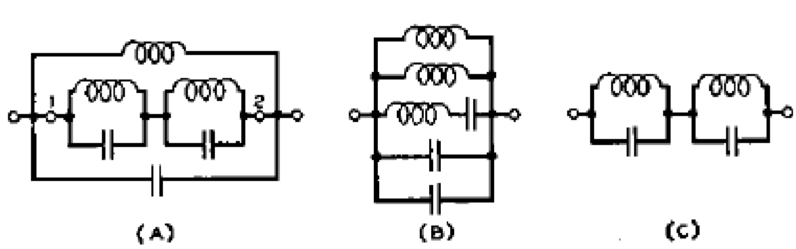


FIG. 65.—ILLUSTRATING HOW A NETWORK WITH AN EQUAL EXCESS OF COILS AND CONDENSERS MAY BE REDUCED TO SIMPLEST FORM BY MEANS OF EQUIVALENCES.

Figure 31: equivalent circuits, 1929

Wiring diagrams were transforming into more than a convenient way to convey information about apparatus. They began to resemble much more what historians of science have labelled paper tools:[522] Discernible in the above is one of the important ways in which concepts of 'equivalence' accrued fundamental importance as analytical, diagrammatic devices. As real things, networks, and systems grew ever more intricate, they provided formal means of simplification and making manageable the real-world complexity of electrical objects - including the bioelectrical ones.

The concept of 'equivalent circuits' then indeed made a career far beyond the confines of the electrical engineering profession. Not, in fact, very surprisingly so: In electro-acoustics, for instance, the 'subtle assistance' provided by 'electrical analogy' came about, as the British wireless engineer Eccles noted in 1929, because 'the study of electrical vibrations in well-defined electrical circuits is easier and has been more cultivated (for practical purposes)'. And as 'vibration phenomena of all kinds approximately satisfy the same linear differential equations', problems concerning vibrations - oscillatory phenomena – thus were best 'translated into problems concerning electrical networks'.[523]

Reflecting such incursions of practical knowledge, electrical analogy reformatted the understanding of the living components of such circuitry as well. Not only would a

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[522] M.J. Nye (2001); Klein (2001); Warwick (2003); Kaiser (2005); Jones-Imhotep (2008).
[523] W.H. Eccles (1929): p.233.

basic familiarity with this diagrammatic language have been essential to understand the behaviours of one's apparatus. Reading a circuit diagram meant, not least, to transpose electrical phenomena – infinitely fast – into a structured space, and to trace their propagation through branching and reconnecting lines, through resistors, capacitors and the other structural elements that made up the functionality of such a *system*: an apparatus, a telephone network, or, as was the case in biophysics, a hybrid, techno-organic assembly composed of living and electric materials. It was, though in a different medium, a movement paralleling the one pointed out already. Would models such as Holzer's make salient the *spatio-temporal* dimensions of bioelectrical phenomena rather than the law-like correlations between stimulus and response, the diagrammatics of circuits instructed one to *see* in such manners. And the remainder of this chapter will examine, essentially, how these things - models and circuitry - came together in practice and concretely: models-in-use of living structures as circuitry. As circuit elements to-be-measured, biological materials turned into (literally) technical objects, and they were represented, almost naturally, by 'equivalent', but readable, structures. Nerve was only one of them.

Substitutions

The following sections return in detail to models, and ultimately, to Cole and Curtis' tracing at the outset: a sudden change of resistance during the nervous action. Practical investigations of the kind a Fricke or Holzer pursued, and, as we shall see, many more of an essentially similar type, had prepared and had played into this fundamentally electrical fabrication of the impulse. And so did, accordingly, high-frequency currents; like no other form of current did high-frequency currents shape and define the study of bioelectricity in the interwar period.

The many 'triumphs' of the vacuum tube, exemplar of 'modern universal instrumentality' prominently included the 'production' of exactly these currents - 'of any desired frequency'.[524] For physiologists, too, there was triumph; for us, it is a barely visible one, for it was about a means of intervention, not of inscription. Earlier the taming, as it were, of alternating currents - their precise production and control - had been problematic, in general. In biological experimentation, their appeal was further diminished by their conspicuous failure to elicit excitatory effects.[525] In theory at least, this absence of stimulatory effects made conceivable alternative forms of intervention, though by and large physiologists were content with what was approved and established, *stimulation* by direct currents. But electro-biologists lost little time to avail themselves to the new - and newly precise - abundance of currents during the 1920s. They then took up for real the project of bioelectrical resistance measurements or devoted themselves to the various effects high-frequency currents were found to provoke, or seemed to provoke, after all. Especially the new 'ultra' high-frequencies fuelled the biomedical imagination. At Harvard, Joseph Schereschewsky of the Office of Cancer Investigations of the US Public Health Service and the physician Erwin Schliephake in Germany, for instance, began to investigate the therapeutic action of such electrical waves with small animals and 'inanimate models' still in the 1920s. More spectacularly, it were figures such as the exiled Russian engineer George Lakhovsky ('the well-known French scientist') who revealed the 'new applications' of such short wave-length oscillations. Lakhovsky's own one materialized, along with a new 'theory of life', as *Radio News* reported in 1925, as the Radio Cellulo-Oscillator. This device, producing currents up to 150 million cycles-per-second, reportedly had a morbid action on plant cells, tumours and microbes too, and it provided the technological substrate for

524 Ibid., pp.232-233.

525 This puzzling absence did prompt a great deal of investigatoins even prior to WWI, sometimes with significant results in fact. In this connections, see esp. Nernst (1908).

Lakhovsky's many assaults on 'orthodox medicine' such as, notably, *The Secret of Life* (1925) and *The Cellular Oscillation* (1931).[526]

Far more significant, because finding far more widespread utility, were the less drastic effects of high-frequency currents. Most prominently, this concerned the production of heat, or what was known as *dia-thermy* (or *thermo-penetration*). The means were the same, but the end not destruction. Rather, it was the useful distribution of currents through bodies, as a British textbook, *Diathermy: Its Production and Uses* (1928), explained:

> To generate a perceptible and measurable amount of heat in the tissues, a current ... deprived of its power to stimulate the excitable tissues and to cause chemical (electrolytic) change [must be used]. This can be done by making it alternate at an exceedingly high rate. ... it may be regarded as not less than 500,000 per second.[527]

The thermal effects induced in biological tissues by alternating currents, noted by Tesla as early as 1891, now provided a therapeutic means, diathermy proponents had it, almost as 'natural' as the 'technic' behind them was radiating with 'intense modernism' and rationality alike.[528] By the late 1920s, so-called diathermy 'undoubtedly occupied the prime position among the electro-physical therapies.'[529] 'There [was] scarcely a region of the body to which it ha[d] not been applied'. [530]

In 1930, in yet another technological upheaval, W.R. Whitney, the perceptive director of the GE research laboratories, hit the news with his discovery that 'men working in the field of a short wave radio transmitter were having fever.' Whitney promptly re-recruited Helen Hosmer, Fricke's former Cleveland colleague to investigate these cases of 'radio fever'. Equipped with 'powerful radio equipment', Hosmer indeed recreated the phenomenon with ease, in both tadpoles and salt-solutions. The medical 'value' of heat being well established (not least thanks to diathermy), such 'artificial fever' quickly found a

526 See Lakhovsky (1925); Lakhovsky (1939): translator's preface.
527 Cumberbatch (1928): pp.3-4.
528 Baker Grover (1925): pp.3-4; on the historical background, see Nagelschmidt (1921): pp.4-6; Kowarschik (1930): p.3.
529 Henseler and Fritsch (1929): p.5; Kowarschik (1930); Cumberbatch (1931a); Cumberbatch (1931b).
530 Cumberbatch (1931b): p.281.

sizeable medical following.[531] By then, diathermy apparatus, whether for clinical use or private practice, were standard items in the catalogues of medical supplier. The pertinent journals, the *British Journal of Physical Medicine,* for instance, were littered with reports and advertisements; its principles routinely explained in physiology courses - even in the islands of scientific purity such as Cambridge University.[532]

In 1929, the physician in charge of the x-ray department of the Addenbrooke's Hospital, Cambridge, described his 'model institute' (which actually existed in Frankfurt-on-Main) thus: 'The basement is given up mainly to diathermy, ultra- violet light, and to photographic work other than the actual developing of X ray films. There are six cubicles for diathermy, while for light treatment there are four double cubicles and a large room for children.'[533] These were the real and concrete spaces where medico-physical agents were converted into spatial, biophysical phenomena, patients became components of circuits, and currents were distributed through bodies. When seven years later, in 1936, the Sixth International Congress of Physical Medicine was staged in London, an entire day would be devoted to diathermy and ultra-short-wave diathermy. Despatched from the GEC Research Laboratories, Wembley, B.S. Gossling on the occasion 'considered in electrical terms' the therapy situation: 'the oscillation generator, the coupling, the application system including the electrodes, and the patient.' Some 'essential differences of outlook between electro-engineering and therapy' aside, a 'simple calculation' revealed that a 200-watt generator produced heat at the rate of approximately one degree per minute in twelve pounds (assuming the patient 'amounted to some 10 ohms of resistance'). To avoid dangerous 'conditions', and to secure optimal results, Gossling here reiterated what had long become a received doctrine: it was all essential to understand how this energy *spread* through the

531 E.g. Stafford (1930); Carpenter and Page (1930); Simpson (ed.) (1937); Rajewsky and Lampert (eds.) (1937).
532 E.g lecture notes 'Easter Term, 1930', entry 'Physiological effects of diathermy', ROUGHTON/APS, Box 34.40u.
533 FFrangcon (1929): p.1239.

body.[534]

To provide such understanding was the power of the electro-engineering outlook. Under its gaze had been created a field of phenomena which was framed by measurement, circuit-models, and biophysical actualities, not by a regime of stimulus/response/inscription. By the mid-1930s, the problems discussed by Gossling had turned routine. Much the same questions occupied, for instance, the attendants of a conference at Dessauer's *Institute for the Physical Foundations of Medicine*, Frankfurt, the following year, in 1937.[535] Its topic: heat-therapy, in 'Research and Practice'. Its 'scientific substantiation' in particular presented a chief biophysical problematic, or so reported Russian émigré Boris Rajewsky (soon to be appointed first director of the new KWI for Biophysics): the effects of electrode size, shape and arrangement on 'current administration', questions of dosage, and, most fundamentally, 'the distribution and conversions of the high-frequency energy in living tissues.' As to this - the probable nature of 'inner mechanism[s]' - there had been, at last, emerging a 'total picture'.[536]

And according to this, the 'body' connected to the 'therapy circuit [Behandlungskreis]' was 'used, as it were, as a dielectric' (i.e. an insulating, non-metallic material). Clear deviations existed between this 'so to speak, purely electro-technical interpretation' and the conditions encountered when dealing with biological tissues. Additional factors, as Rajewsky cautioned, 'macroscopic' structures, then influenced current distributions and energy conversions.[537]

Nevertheless, construing such *use* of the body in terms of dielectrics was as theoretically illuminating as it was practically mandatory. From these frequency-dependent bodily properties important inferences could be drawn about the likely efficacy of currents of a given frequency, their localisation, and depth of penetration. Fortunately, analytic

534 nn. (1936): p.1203.
535 Rajewsky and Lampert (eds.) (1937); on the Institute, see Dessauer (1931).
536 Rajewsky and Lampert (eds.) (1937): p.XII; p.80.
537 Ibid., pp.83-84.

models for such 'inhomogeneous' dielectrics could also be derived through analogous, somewhat more 'complicated' considerations pertaining to *simple* organic systems. These were the high-frequency investigations of the kind we already have encountered: investigations in the manner of a Fricke or Holzer, and thus the ways, say, a red blood cell could be 'electrically represented'. In Rajewsky's example: a resistor and capacitor (cell interior), couched in between two capacitances in series (the membrane), and in parallel to this, another resistor and capacitor standing in for the external medium (the serum).

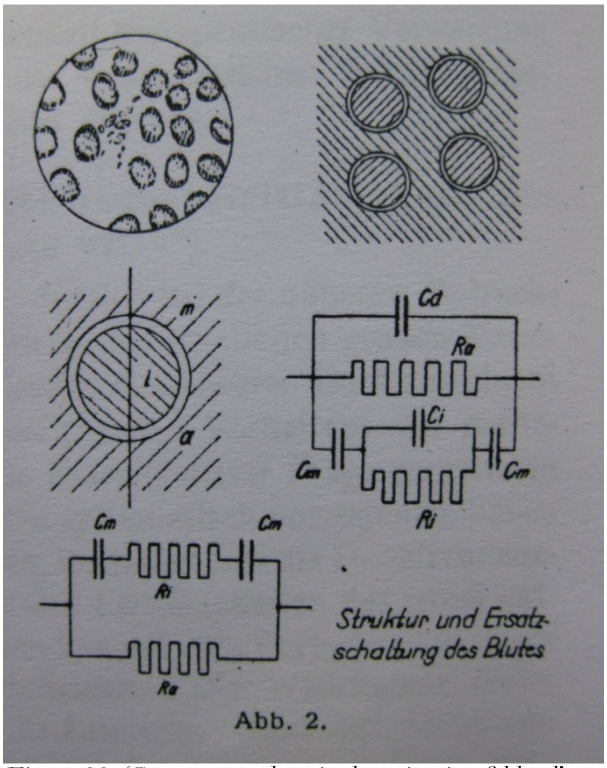

Figure 32: 'Structure and equivalent circuit of blood', 1937

In these ways, mediated through circuitry, and through several layers of *ersatz*, diagrammatic models, biophysical model-objects, and the practice of physical medicine came into intimate contact. Ersatz, or circuit equivalence, was programmatic: integral to practice, and essential in terms of making intelligible the operations of currents in biological bodies. This particular *Ersatz-schaltung* thus illustrated the biophysics of alternating currents in a 'relatively simple' manner: at low frequencies, Rajewsky explained, polarisation phenomena occurred in the dielectric material of 'membrane', effectively creating an insulator therefore; at higher frequencies, these insulating phenomena would gradually fade and rapidly oscillating charge movements occur in the cell interior. The result: thermal effects.[538]

In pushing the field towards its physical foundations, Rajewsky certainly belonged to the more academic end of the knowledge-production spectrum. But he was hardly an isolated figure. The immense literature on diathermy and kindred applications was traversed by calls for 'rational' therapy and controversies surrounding its physical *foundations*. Text-books on the subject routinely explained the nature of electricity and its biological effects, replete with helpful 'diagrams' through which the 'difficult subject of electrical reactions' was 'elucidated'.[539] Biological effects were brought nearer with the aid of equivalent circuits; and in ways even more palpable, one illustrated the influence of electrode shape and size on current distributions: In protein solutions, gelatine or meat, high-frequency currents left their visible traces - zones of coagulation:

538 Ibid., pp.83-86.
539 nn. (1930a): p.140.

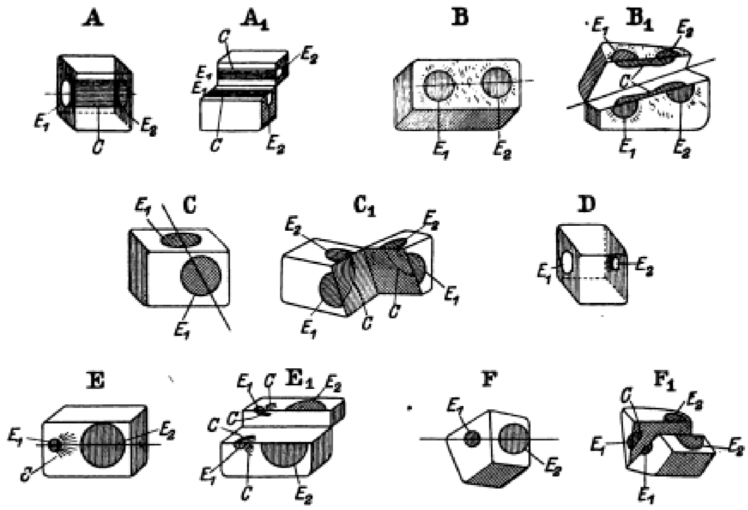

Abb. 41. Schema der Stromverteilung im Gewebe, durch Koagulationszonen (schraffiert) gekennzeichnet.

Figure 33: coagulation zones, 1921

The clinical applications of high-frequency currents were surrounded by model-experiments: concrete, material substitutions. The spatio-temporalities of 'heating effects' had for the most part been studied 'in vitro', preferably through 'the coagulation of egg albumin or the cooking of meat and potatoes', as one medical scientist complained in 1927, their workings in living system only inferred by 'analogy'.[540]

Indeed it was not long until the more abstractly-minded biophysicists intervened and shifted matters of substitution towards more formal planes. Professor of Physiologic Chemistry at the University of Minnesota Medical School, Jesse McClendon, for instance, also belonged to those who desired more rigorous approaches to these current *distributions*. 'The extensive use of high frequency currents for heating the deeper tissues of the human body', as McClendon submitted in 1932, 'has made it desirable to obtain more information on the path of the current between the electrodes and the distribution of heat in the tissues.'[541]

It didn't mean less concrete. On McClendon's mind, it was the 'localization of

[540] Binger and Christie (1927): pp.571-572.
[541] Hemingway and McClendon (1932): p.56.

heating [that] is important'. And therefore, to know the 'seat of the ... resistance'. The path towards progress McClendon opted for, meanwhile, was well trodden. It was the path of high-frequency measurements, and thus the path of Fricke, Holzer, and innumerable chemists and electrical engineers. Having extensively studied the electrical properties of sea urchin eggs, muscular tissue, and blood suspensions, McClendon already had convinced himself that a 'true reproduction of the circuit within the cell' could be obtained - with the appropriate methods. And here, as it were, we approach the heart of the matter where models, circuits, and instrumentation merged with the object of investigation. For, such required 'bridge' circuits - 'most extensively used by physical chemists, industrial chemists, and workers in biological sciences' - as an assistant of McClendon's explained in a 1927 review of the subject (which treated especially on the beet root).[542]

Their basic principle was simple enough, and, in fact, long established. It left few traces, because the goal was silence - the *absence* even of sound: Equipped with a telephone, when measuring with a bridge-circuit one was required to 'balance' an unknown circuit component (or 'arm') against a parallel, *known* one: Silence meant balance. For decades investigators had confined themselves to determine the unknown resistance (for instance, of a piece of nerve), Mr. Remington (the assistant) observed, even though often 'silence could not be obtained in the telephones'. One encountered 'troublesome' effects, and these, one naturally assumed, had 'to be gotten rid of before accurate bridge readings could be taken'.[543] Gradually, however, in the course of the 1920s, a much more complex picture of the conditions in such electro-organic circuits had emerged. Investigators thus had come to appreciate the *systematicity* of these effects. This owed everything to the increasingly wide range of frequencies at their precise disposal.[544]

Far from being troublesome, with the electronic art of frequency control, so was

542 Remington (1928): pp.353-354.
543 Remington (1928).
544 Esp. Ebbecke (1926); Bishop (1927); McClendon (1927); Gildemeister (1928); Fricke and Morse (1926); Cole (1932).

revealed in addition to the object's resistance, the presence notably of a 'capacitance' effect. It made itself suspiciously manifest at the far, high-frequencies end of the spectrum. The implication was that neither of the simplistic, 'customary methods of obtaining balance' in a bridge thus resulted in a 'true reproduction' of the unknown 'circuit' that was the cell. At the very least, the more complex 'picture' would involve, according to what quickly turned into the consensus view, a resistance (the cell interior) in series with a 'leaky' condenser (the cell membrane):[545]

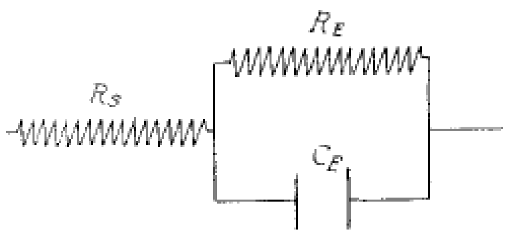

Fig.3

Figure 34: 'leaky condenser', 1928

Once established, such circuit representations could be turned to manifold uses. Gauging current distributions, and devising means to control and improve it; diagnosing malignant tissue; or, based on measured, empirical values of conductivity, the thickness - its real, physical dimensions, of cellular membranes (one that had to be postulated as the source of the resistance) could be estimated.[546] It was, in other words, through this material logic of substitution, inherent to the techniques employed, that the more fundamental perspectives on the physical properties of cells were gradually developed, and the differences of things living and technical submerged in the equivalence of cells and circuits.

[545] Remington (1928): pp.356-358.
[546] On the formal details, see e.g. Fricke (1932).

Invading the laboratory

In the world of cellular circuitry that had been crafted in the period following WWI, high-frequency practice – almost as universal, after all, as the vacuum tube - made salient, as we have seen, not the laws of nervous excitation, the dream of classical electrophysiology. Instead, it were the spatio-temporality of current distributions, the structural complexity of biological tissues, and most of all, their physical properties. It was a shift of registers and focus prompted by the practical problems that high-frequency interventions into 'biological materials' posed. And the following returns us to the particular application of high-frequency currents with which this chapter has opened: the nerve membrane. It also means to return to Kenneth Cole and his assistant-collaborator Howard Curtis - they too were products of this practice-bound bioelectrical arts. In fact, both their paths had fatefully crossed those of Hugo Fricke's.

Fricke's own initiation into biophysical research, as seen, took place in a world of blood suspensions, breast tumours, pathological conductivity changes, and x-ray dosimetry - all held together by Crile's encompassing vision of the bioelectrical nature of life. His approach to the electrical properties of cells, like the circumstances, didn't differ in principle from those of other investigators: A high-frequency 'bridge', suspensions of cells, circuits, simple models. The relatively larger impact Fricke in fact had on the biological community may partly be explained by his expertise, as a physicist-engineer, with the principles of measurement and electrical theory. More interestingly, as noted, Fricke quite suddenly found himself transplanted into the centre of academic, 'quantitative' biology, the renowned home of the Cold Spring Harbor Symposia on Quantitative Biology. The first, five years after Fricke's arrival in Long Island in 1933, appropriately enough, dealt with *Surface Phenomena*. Fricke himself discussed the 'Electrical Impedance of Suspensions of Biological Cells', which now reached a tremendously broader and different audience than any paper on breast tumours ever might have.[547]

Present during this first summer of meetings were the likes of Herbert Gasser, Osterhout, Eric Ponder, Leonor Michaelis, as well as Kenneth Cole – biophysicists, for the most, of present or future acclaim: the 'presence of such a group ... each summer', as the published Symposium volume announced, would hopefully 'aid the Laboratory in its ... aims of fostering a closer relationship between the basic sciences and biology.'[548] Henceforth, Fricke would converse with the luminaries rather than crackpots of quantitative biology, and breast tumours be replaced by more respectable objects of investigation. The publications now issuing from Fricke's circle bear the marks of his newly biological environs: 'The study of the electric resistance of living cells', as one of Fricke's new students surmised in 1931, 'has been used chiefly in ... special investigations on subjects such as the resistance of malignant tumors; but such problems of general physiology as growth or death, in relation to variation of frequency, remain almost untouched.'[549]

Here we can see an effect, or a technique, invading the laboratory, not escaping it. Cole too, who by then had moved on from an apprenticeship with Fricke's at Crile's Cleveland Clinic to Harvard and eventually to a position at Columbia University had undergone a similar trajectory. And Cole too is best construed, as we shall see, as the same sort of bioelectrical bricoleur rather than the Harvard-trained Columbia professor.

The more academic - and natural - environs wherein which they came to operate did shape, of course, the investigations whose eventual product was the seminal tracing - the one at the opening of this chapter - of an impedance change of the nerve membrane as the impulse travelled along the nerve fibre. There would be little plausibility in reducing this or any account of such objects as the nerve impulse to nothing but practicalities, things

547 Fricke (1933).
548 nn. (1933): p.v.
549 Luyet (1932): p.283.

and contexts not normally considered part of the story. And the point, like in the preceding chapters, is not to reduce them to medical physics, but seeing them as intertwined, always and everywhere, with only seemingly unconnected, and only seemingly sterile, merely practical contexts of biophysical science. Fricke's relocation can illustrate here quite well this shift towards problems of a more functional, 'general physiological' nature. It would partly precede, partly parallel Cole and Curtis' own moves into general physiological territories.

Even in Long Island, Fricke retained a preference for the simple red corpuscle - albeit with a new emphasis. Fricke then moved beyond the merely *static* properties of membranes. It was the result of a complex set of factors: progress in high-frequency technique; the interaction with biological students who came to the picturesque location for summer school or more permanently to be 'acquainted at first hand', as Fricke said, with the 'findings' of biophysics; and not least, the Long Island site - a strategically located nature-spot, 'easily accessible to biologist resident in, or visiting, New York, and to those in passage to and from Europe.'[550]

Fricke's regular interlocutors then began to include such figures as Osterhout or Danielli whom we will remember as significant agents in matters of membranes. And having recruited, notably, the electronics-savvy Howard Curtis above, a recent Yale physics graduate, the two of them soon were able to observe variations in the frequency-dependent electrical characteristics of the cell as they induced membrane 'desintegrations' through swelling in water (osmotic lysis), by way of freezing and thawing, and with various chemicals. 'The fact that a change of the frequency dependence takes place', they first reported in 1935, 'show[ed] that the injury cannot be due merely to a rupture in the membrane, but must be due to changes in the properties (increased permeability) of the

[550] Fricke, memorandum 'General in Biophysics', August 1930, FRICKE/CSH, folder 'Dr Hugo Fricke' (folder 3/3)

membrane as a whole.'[551]

The potential significance of these new horizons was clear enough – one observed physiological, functional *changes*. Meanwhile, making intelligible these membrane behaviours was, as ever, difficult. Not everything here was nature, pure and complex. As a supplement to these physiological forays, Fricke availed himself to even simpler, fabricated systems. Clearly, certain 'characteristics' of nature's surfaces were easily 'obscured ... by reason of their lack of homogeneity'.[552] Fricke's surviving notebooks, in turn, show him grappling with various 'model substances': On December 17, 1934, for instance, Fricke prepared 'Heavy suspension of whipping cream in H_20'. January brought 'Lion brand evaporated milk-homogenized' and solutions of '1% of "Cooper's" gelatin'.[553] Or again, suspensions of (relatively simple) yeast cells, it was found, very distinctively exhibited sudden, drastic drops in resistance and capacitance at high frequencies, while otherwise, these properties remained fairly constant over a wide range of frequencies.

Such systematic – and reversible - behaviour indicated *functional* changes. These sudden changes unlikely were due to merely 'a minute disintegration' of the lipoid layer surrounding these cells.[554] Fricke, meanwhile, struggled with the detailed interpretation of these observations, jotting down calculations next to circuit diagrams, wondering about 'condition[s] of equivalence':[555]

551 Fricke and Curtis (1935): p.836; on Curtis, see Zirkle (1972).
552 Fricke and Curtis (1935): p.836.
553 See Notebook V, FRICKE/CSH, Box 2, folder 'Fricke Notebook, Book V'
554 Danielli and Davson (1935): p.506.
555 See Notebook II, FRICKE/CSH, Box 2, folder 'Fricke Notebook, Book II'

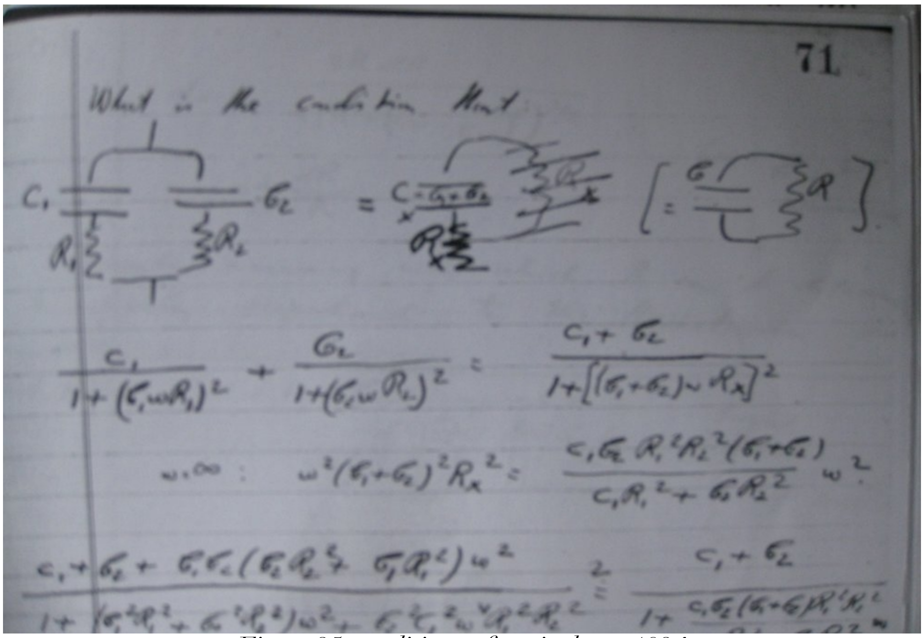

Figure 35: conditions of equivalence, 1934

Making intelligible membranous behaviour – the organic component of the measurement circuit - was a *multi-layered* process of substitutions. In the bridge-circuit technique, *ersatz-schaltung* was built in, literally. Simpler objects, whether whipped cream or gelatine, were another route of modeling by way of material *substitution*. Electricity (and its diagrammatic language) being the universal tool that it was, results obtained in other places and on other things were enrolled - with ease: 'For soils, various investigators concerned with the problem of radio communication', as Fricke duly noted, have found quite similar frequency-dependent electric behaviour which 'probably [was] of the same type as that studied here.'[556]

And there were, of course, also part of the circuit patients, malignant tissues, blood serum, microbes, bacteria, heavy cream and skimmed milk. The corresponding 'electric diagrams', once extracted, were further processed, transformed, simplified, and calculated with - a process that eventually fed back into measurement-practice again because measuring precisely required knowledge of what one measured and being able to filter

[556] Curtis and Fricke (1935): p.775.

significant behaviour from mere noise. These diagrams, especially the ones that never made on the pages of circulating journals and books, were never only static, formal representations or abstractions, but analogical devices *used*. We may indeed think of these material alignments of ersatz along the lines of the deflationist, inscriptions-practices-centred notion of 'abstraction' and 'theory' Latour's *Science in Action* famously developed in his account of 'centres of calculation'. Or more pertinent perhaps, along the lines of the 'successive layers of transformations' between and among inscriptions – notes, charts, diagrams and so on – which Latour has advanced as an account of *representation* elsewhere.[557] On this account, inscriptions do not *represent* reality. Neither did, of course, the models and circuitry biophysicists were producing and dealing with. The difference is that in the picture of (biophysical) science in action presented here, inscriptions, representations, the visual and textual/graphic do not play the fundamental, all-defining roles.[558] Rather, accompanying and preceding these operations of writing and reading, there were things, interventions, sounds, material substitutions and ersatz-objects all assembled together by what I argued were historically specific cultures of (apparatus) *use*.

And from here, taking a step towards the electrical phenomena of nervous activity was merely a matter of yet another application - or almost. Fricke himself, being adept to this electrical, material world, was able to generate increasingly better guesses at the physical dimensions of these – possibly bi-molecular – cellular membranes. The exact 'meaning' of these measurements, for the time being, proved somewhat elusive. No clear 'conception as to the origin of the dielectric properties of cell membranes', as Fricke confessed in 1937, was in the evidence, and neither was it, of their *changes*.[559] It was not for Fricke, at any rate, himself increasingly consumed with problems of radiation biology, to carry this particular

[557] Latour (1987): esp. pp. 241-243; Latour (1999): chapter 1, esp. p.64.
[558] On Latour's quasi-theological obsession with the written, also see esp. Schmidgen (2008).
[559] Fricke to Osterhout, 18 February 1937, OSTERHOUT, Box 2, Folder 'Hugo Fricke'

case forward - eventually, towards the mechanism underlying action potentials in nerve in the 1940s and 1950s.[560] The detailed story of these potentials will be the subject of the next two chapters. Here, we can end, simply, on the slightly protracted migration of high-frequency measurements towards the nature of the nerve membrane in the hands, notably, of Kenneth Cole (though there were others). It was a small step in this world of circuitry; but an essential one towards everything, in matters of nerve impulses, to come.[561]

Becoming a nerve-biophysicist, circa 1925-1935

When Fricke and Curtis first broached the high-frequency behaviour of functional changes, nerve was still a problem very marginal to Cole's biophysical interests. His eclectic trajectory indeed is but a variation on the foregoing. Born in 1900, Cole grew up in Oberlin, 'hanging out' during high school at a local telephone company 'accumulating batteries, magnetoes, and other worn out parts'.[562] It resulted in Cole's first 'licensed' radio station, and less hobby-esque, Cole spent two years at the GE Research Laboratory, Schenectady, before enrolling, in 1922, as a physics graduate at Cornell. The next year, Cole, in search for a summer job, responded to a fateful note hung up in the physics department: 'Wanted, at the Cleveland Clinic, two biophysicists'.

Despite his ignorance, Cole found himself admitted to Crile's circle, assisting Fricke in conductivity and x-ray investigations. Intrigued, Cole spent the next summer at Woods Hole working on the heat production of sea urchin eggs, and he would return once more to Cleveland in the summer of 1925. Meanwhile, Cole hastily finished his PhD on the behaviour of low speed electrons, and a NRC post-doctoral fellowship sent Cole to

[560] On Fricke's further trajectory, see A.O. Allen (1962); Hart (1972).

[561] Cole wasn't then the only physiological scientist who carried alternating currents into the domains of general physiology. But, for a number of reasons, Cole's contributions would prove the most central. Especially noteworthy in these regards are the contributions by the Germans Martin Gildemeister, an authority on the electro-physiology of skin, and Hans Lullies. See e.g. Lullies (1932).

[562] Quotes and biographical information, unless otherwise indicated, come from the NIH oral history collection, Miles (1972).

Harvard, to work, jointly, with Emory Chaffee at the High Tension Electrical Laboratory, and with W.F. Crozier of the Department of General Physiology.

Crozier's department, as Pauly has shown, was one of the few successful attempts to implement the '"Loebian" spirit' in a major academic, institutional setting, Crozier himself having obtained his PhD under Osterhout and already having honed his 'physico-chemical' outlook on biology as a technician at the federal Bureau of Fisheries.[563] Chaffee, for his part, was not only an authority on vacuum tubes but regularly weighed in his opinions (often accompanied by experimental results) in biophysical matters as diverse as the sterilization of fruit juices, 'ultra-violet' therapeutic lamps, iono-atmospheric hygiene, or 'diathermy from the view point of physics'.[564] But notably 'Hearing The Eye See', as the *Scientific American* reported in 1929, was possible thanks to Chaffee who had pioneered recordings of retinal action currents with the aid of amplification (and a telephone).[565] While at Harvard, Cole himself began to 'duplicate' Fricke's high-frequency bridge. His first publications on the electrical impedance of 'Suspensions of Spheres' - sea urchin eggs - appeared in 1928 right before Cole left, on a Rockefeller grant, to Leipzig. There, Cole was to work with Peter Debye, who, in collaboration with Erich Hückel, was then at the forefronts of advancing the theory of electrolytes.[566] Equipped with the latest knowledge on ionic phenomena, Cole accepted, upon his return in 1929, a position as assistant professor in physiology at the Columbia College of Physicians and Surgeons, where he would remain until 1943.

Not surprisingly, Cole's forays into biophysical matters, employing the conveniently simple, almost spherical eggs of the sea urchin *Arbacia*, were as biologically unromantic as they were inclined towards theory. But Cole's theoreticality was grounded in practicalities –

[563] Pauly (1990): esp. pp.183-185.
[564] See Cruess to Chaffee, 15 January 1932, CHAFFEE, Box 1, Folder 'C'. And see Chaffee's correspondence esp. with Osgood, Box 2, Folder 'O'; with Yaglou, Box 2, Folder 'Y'; and with McFee, Box 2, Folder 'M'
[565] Chaffee to Moriondi, 10 January 1929, CHAFFEE, Box 2, Folder 'M'
[566] On the rapid advances in this connection, see e.g. Nielsen and Kragh (1997): esp. pp.315-317.

the theoreticality of the electrical engineer rather than the physicist's.[567] Not least, they show Cole deeply concerned about the 'limitations of impedance measurements'. It was 'evident', Cole thus pondered in his discussions of the circuits that represented his sea urchin eggs, 'that ... the number of circuits which can be made to fit a given set of data is probably limited only by the patience and ingenuity of the computer.'[568] No hard and fast conclusions could be drawn from impedance measurements about the actual distribution of electrical elements, Cole alarmed, referring readers to a recent publication on the 'Theory and Design of Electric Wave Filters' by Bell labs engineer Otto Zobel.[569]

Despite such qualifications, circuits, having accompanied Cole's doings from his school days, were the end-all and be-all of Cole's biophysical gaze. To Cole, they revealed structure within the confusing, uncertain world of bioelectrical phenomena. Another Bell labs engineer, K.S. Johnson (at the time a visiting professor at Harvard), had initiated the young Cole to the higher knowledge of equivalent circuits: For a given frequency range, two electrical networks are equivalent if and when their impedance and phase angle (the phase shift between voltage and current) are identical.

The productivity of such electro-technical insights promptly were revealed in a follow-up paper on the 'Electrical Phase Angle of Cell Membranes' in 1932.[570] Drawing together a large range of impedance data, Cole showed that in all these cases - suspensions of calf blood, nerve, muscle, cat diaphragms, skin, potato slices – while the impedance varied with frequency, the phase angle remained very nearly constant. From the perspective of electrical networks, as Cole explained it here, a non-constant phase angle would have implied a complex arrangement of impedance elements. The evidently constant phase angle meant, however, that in all these cases fundamentally the same – and simple - conditions prevailed.

[567] Cole (1934): pp.164-165; on the practical-theoretical background of the kind of mathematics that was brought to bear here on nerve, see esp. Mindell (2002): pp.107-110 .
[568] Cole (1928): pp.34-35.
[569] Cole (1928).
[570] Cole (1932): esp. p.649; Miles (1972).

Order from chaos: the 'significance' of this was that all these cases, whether one dealt with simple blood suspensions or complex tissues, could be reduced to – were equivalent to - a circuit containing only a 'single variable impedance element'.[571] At the 1933 Surface Phenomena symposium in Cold Spring Harbor, Cole had little time for the only apparent complexity of 'biological systems'. The 'frequency characteristics of tissues', as Cole informed his biophysical peers, were unlikely due to 'distributed effects'. Rather, they were due to a single element, the 'variable impedance element of living tissues'; its 'seat', Cole confidently declared, '[wa]s probably the cell membrane.'[572] Evidently, not only was 'this type of analysis' 'useful' when studying the response behaviour of organic materials.[573] It also pointed Cole invariably towards the cellular membrane as the principal agent in bioelectrical, vital phenomena.

As these convictions grew, Cole was settling in at the Department of Physiology at the Columbia College of Physicians and Surgeons, a place that entangled Cole even deeper (and diversely) in the borderlands of physics and medicine.[574] Cole's appointment had been engineered by Horatio B. Williams, American pioneer of electrocardiography and a renowned student of electric shocks ('Life is beset with hazards').[575] With Williams' support, Cole himself soon got involved with a project on electrical shock with the 'telephone people' at nearby Bell Labs, and as 'consulting physicist' Cole was put on the staff of the X-ray department at Columbia Presbyterian Hospital. Cole found himself, in addition, launched on a NRC Committee on Biological Radiation, henceforth busy, as he wrote to Chaffee, compiling 'general methods for the production and the measurement of the radiation absorbed [by biological tissues] for all wave lengths.'[576]

Cole's biophysical life, in short, took the somewhat haphazard, eclectic shape that

[571] Cole (1932).
[572] Cole (1933): pp.111-115; Miles (1972).
[573] Cole (1934): p.165.
[574] Note 'Monday , Sept. 16, 1935. Dr. Kenneth Cole', RF/RG.1.1 Series 200, Box 133, Folder 1650
[575] Root, Kruse, and Cole (1956); cited is H.B. Williams (1931): p.156.
[576] Cole to Chaffee, 30 April 1934, CHAFFEE, Box 1, Folder 'C'; and Miles (1972).

should be familiar by now, distributed in between the fluid but wired boundaries of medical physics, marine laboratories, and radio engineering. Meanwhile too, Cole had won the attention of Warren Weaver, and had submitted, still in 1935, to the Rockefeller Foundation a 'program of research on the electrical constants of the membrane and cytoplasm of the normal and abnormal cell.'[577] The program, not failing to promise significant pay-offs for medicine, found approval, Cole evidently being eager to chart out more complex terrains. Indeed, at the time Cole also ventured, in collaboration with a Columbia anatomist, into the analysis of embryo rat heart muscle cultures – most active cells. Little could be made, however, of the heaps of confusing data they produced. With the German Emil Bozler, a trained zoologist then on visit at the Johnson Foundation for Medical Physics, Cole took on impedance changes during muscular activity and rigor, but these proved similarly elusive: The 'theoretical muscle', Cole and Bozler mused, was a complicated thing: it 'will be a uniform, random distribution of parallel circular cylindrical fibers in a medium.'[578]

The active behaviour of these complex, bioelectrical objects all-too-easily sabotaged the aim of investigating the functional changes they quite evidently underwent. Cole, for his part, had already been watching out for simpler conditions: The 'most direct attack', as Cole had surmised in his contribution to the Symposium on Quantitative Biology in 1933, would be relinquish such complex materials altogether, and to measure the impedance 'between the interior and exterior of a single cell ... such that the most of the current traverses the cell membrane'.[579]

The prospects were daunting, however.[580] At the time, only a very few investigators had barely felt their way towards 'single cells'. The required, minuscule micro-electrodes were by and large a technology of the future. Still, biologists routinely worked on isolated

[577] Hanson to Bronk, 2 October 1935, RF/RG.303, Box 52, Folder 19; Cole to Gentlemen, 23 September 1935, RF/RG.1.1 Series 200, Box 133, Folder 1650

[578] Bozler and Cole (1935): p.231; Miles (1972).

[579] Cole (1933): p.111.

[580] See Cole to Gentlemen, 23 September 1935, RF/RG.1.1 Series 200, Box 133, Folder 1650

organs, whole tissues, or suspensions. The 'single cells' that came into question at all, because they were large enough, weren't even real cells but unicellular algae, tulip spores, and marine eggs.[581] They also were very fragile objects, and measuring them in the way Cole proposed meant 'impaling' them – a highly precarious affair. Most troubling of all, with these objects too one was running into certain 'active' effects - even with high frequency currents - 'as distinguished from the 'passive' ones' that one 'always hope[d] to maintain during the measurement.'[582]

All this would have served to render the nerve impulse a far from obvious object of investigation to electrically-minded investigators such as Cole. It was the appearance of two new experimental objects, in relatively brief succession, that principally altered the position. They put the impulsive behaviour of nerve very prominently on the map. One of these objects would make a big career in the biophysical science of nerve indeed, and its origins are something well remembered: In 1936, Cole was introduced to a nerve-axon visible to the plain eye by the young Oxford zoologist John Z. Young who was touring the East Coast on a Rockefeller stipend. 'In spite of their great size', Young noted with some surprise at the 1936 Cold Spring Harbor Symposium on Quantitative Biology, these axons - the giant axon of the squid - seemed to have completely escaped previous investigators.[583]

It was the giant axon, we will remember, that generated the iconic trace with which this chapter began. And, in all its largesse, it will figure prominently in the remaining chapters of this thesis. Here, however, it will be more instructive to focus on the second, and less ennobled object. For, this one, though real and natural enough, too was very much a matter of ersatz: another layer of substitutions.

This other object was a plant: a giant algae to be precise, or rather, the phenomenon that it only recently had been exposed to generate. Thus, in about 1927 its

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581 The earliest attempts to measure such 'single cell' - type items were of very recent vintage. See Ettisch and Péterfi (1925); Gicklhorn and Umrath (1928); Osterhout, Damon, and Jacques (1927).
582 nn. (1933): pp.114-115.
583 J. Z. Young (1936): p.4.

discoverer, W.J.V. Osterhout, had noted an impulse-like passage of electrical phenomena in the algae *Nitella* when injured: A 'wave of some sort', Osterhout proposed, 'which we may for convenience call a death wave'. This death wave, as he perceptively realized as well, clearly 'resembl[ed] action currents of nerve and muscle'. It only travelled much slower.[584]

It was a quasi-nerve, or so it was constructed. And to no small extent, Osterhout's considerable standing as a maker of cell-models had been built on this one 'fortunate finding' on the tropical beaches of Bermuda: large, unicellular algae - *Valonia macrophysa, Nitella, Chara* - some of them reaching the size of a hen's egg. In contrast to the then usual objects of investigation – muscle or nerve *tissue*, the much smaller and less lively red blood cell or *Arbacia* eggs - these were *living, active single cells* (that was, a 'central vacuole ... surrounded by a very thin layer of protoplasm').[585] There was no question, then, as Osterhout had prophesied in 1925, that they should prove a 'powerful instrument of research'.[586]

These advantages, persistently preached by Osterhout, were readily evident, and by the early 1930s, scientists at Woods Hole, Naples and Plymouth were busily studying *Valonia* and *Nitella*. Such 'applications to animal physiology', as Osterhout proudly reported of these algae in 1933, as 'utiliz[ing] the work on plant cells to explain what happens in nerve' were particularly popular.[587] Osterhout, after all, was cultivating his giant algae at a *medical* research institution. But there was little rhetoric and exaggeration here: At the time, Alan Hodgkin, for example – the main cast of the following chapters – was crafting his undergraduate student essays in Cambridge – on nerve physiology - around the excitatory phenomena one elicited from Osterhout's plants; figures such as A.V. Hill and Rudolf

[584] Osterhout and E.S. Harris (1928): p.186 'Report of Dr. Osterhout' (1930), p.15, OSTERHOUT, Box 3, Folder Report 1930.

[585] Osterhout (1922): p.226; 'Dr. Osterhout's Report on Bioelectric Properties of Cells', pp.121-122, OSTERHOUT, Box 3, Folder Report 1927; on Osterhout, see Blinks (1974): esp.p.225; and Pauly (1990): passim.

[586] 'Report on Work in Bermuda' (October 1925), p.9, OSTERHOUT, Box 3, Folder 'Bermuda Project Rockefeller Grant'

[587] Osterhout to Parker, 30 September 1930, OSTERHOUT, Box 4, Folder 'Parker'; Osterhout to Flexner, 10 April 1933, OSTERHOUT, Box 2, Folder Flexner (1/2)

Höber were excitedly championing the object as well;[588] but especially for Cole and Curtis these humble algae proved the intermediary between complexity and simplicity, between the real thing – the nerve impulse - and electric passivity of skimmed milk and sea urchins.

If the possibilities the squid giant axon offered in terms of membrane-analysis were plainly obvious, adapting existing techniques was not. Here, like in twitching muscle or heart cells, electrical effects were fast, intricate, and *active* – working against the established procedures of bioelectrical measurement. For everyone attuned to a world of circuitry, however, and thus, to representing and intervening in terms of electrical equivalent behaviour, the remedy would have come very natural. Replace the elements in the circuit: In 1938, the year before the giant axon was made to reveal its transient change of resistance, the *New York Times* thus reported that

> Drs. Cole and Curtis … [had] discovered that the long single cells of the fresh-water plant nitella, used frequently in gold-fish bowls, are virtually identical with those of single nerve fibers. ... The electrical nerve impulses in the plant were found to be much slower than those in animals. This discovery was seized upon by the Columbia workers ... The nitella plant thus may become a sort of Rosetta stone for deciphering the closely guarded secrets close to the very borderland of mind and matter.[589]

Nitella, it was found, allowed to reproduce the phenomena encountered in nerve, albeit, on a rather different scale. For the first time, an impulse-like phenomenon, a *change* of resistance accompanying activity, had been not so much inferred than measured, in real-time, at slow motion – and in an algae. An ersatz-impulse.

And there is little behind this seizure that was particularly remarkable. Meanwhile, Cole had befriended Fricke's assistant Curtis, and the two of them had spent much of 1934 in sunny Bermuda: simple sea urchin eggs were in ample supply, and Cole and Curtis were honing their high-frequency skills with these simple, robust, if slightly passive and lifeless objects. With the Rockefeller grant in hand, Cole was able to formally recruit Curtis in

[588] E.g. MS 'Membrane Theory' (1934), HDGKN A.59; and A.V. Hill (1932a).
[589] nn. (1938): p.35.

1936. Much efforts then went into an improved high-frequency bridge, optimized for the needs of bioelectrical measurements: it minimized undesired heating effects, and specially 'designed' resistors allowed to *balance* 'biological materials' making the apparatus more appropriate – or equivalent, as it were - to the peculiar nature of organic things.[590] Also in 1936, as the giant axon came along their way, Cole and Curtis first had seriously begun to consider the question of active effects - nervous impulses. The project of taming this object, however, and its complex electrical behaviours, soon lead the two on to this other, more approachable, but almost-equivalent circuit-element: *Nitella*. A Rosetta stone, or more prosaic: an equivalent circuit.

Conclusions

The story has come full circle. Supplemented with extensive studies on *Nitella,* into the electrical fabrications of the nerve impulse went, this chapter has shown, a great many disparate seeming things: algae, high-frequency currents, diagrams, circuitry, and thus, such diverse subject areas as the electrophysiology of lowly plants, but more crucially so, the scenes of medical physics, the electronic arts, and radio-cultural forms of instrument use. As an account of the electrical fabrication of the nerve impulse, this chapter indeed did not particularly deal with nervous phenomena at all. Here, a combination of medical physics and bioelectrical *bricolage* emerged as a key factor in the knowledge production concerning bioelectrical phenomena. 'The experimental procedure and the technique of analysis [were] fundamentally the same as those used in Nitella during activity', as Cole would note in the 1939 paper that accompanied their seminal record.[591]

The story of the nervous impulse, and its models, in many ways, began rather than ended here, in 1939. The remaining chapters will treat on what came out of the squid and

[590] Cole and Curtis (1937).
[591] Cole and Curtis (1939): p.650.

the electronic arts in the ensuing one and a half decades. Deciphering the secret of nerve impulses, as we shall see there, would require, among other things, a further such electronic manoeuvre: it meant stalling in time the impulse itself, to take control, that was, of the action potential as such. However, many of the preconditions, many of them subject of this chapter, it will be important to keep in mind, were now in place. In particular, here we have seen how the electrical expressions of life, far from being merely traces and inscriptions, gradually but definitely and materially were given real substance - as circuitry. Again, it was in relation to these mundane things, the circuitry that pervaded interwar life-worlds, that modeling practices emerged, almost naturally, out of mundane practice.

Thus, returning to the Cole and Curtis' tracing at the outset of this chapter, we can see now how behind this familiar tracing there was hidden a far less familiar biophysical world. The genesis and legibility of this tracing was not only depended on particular interpretational techniques, this morphology of circuits itself was embedded, quite concretely so, in experimental and material cultures that largely would remain invisible were one to adopt the narrow perspectives from academic nerve physiology, nervous signals, or inscription devices. The corresponding circuitry-based modeling practices, reflected the variety of medico-physical practices that surged in the interwar period, and more broadly, I have argued, they reflected the permeation of interwar life-worlds with electrical technologies. They were the images behind the images, as it were: they allowed to read sense, or at least certainty, into the uncertain, noisy, transient phenomena one was generating (and recording) almost as easily as one procured radio spare parts. Bioelectrical phenomena, whether produced from algae or patients, after all, were subtle, intricate and somewhat elusive manifestations of life. More cautionary than the *New York Times* thus went the 'appraisal' of the Rockefeller Foundation when the news of Cole and Curtis' feat made the rounds in 1938. Behind closed office doors, it was soberly noted that there was 'no doubt about the accuracy of the measurements themselves; but some doubt to what one is measuring'.[592] But this appraisal was perhaps not entirely hitting the mark: because the what, no doubt, had an 'equivalent circuit'.

[592] 'Appraisal' (1938), RF/RG.1.1, 200D, Box 133, Folder 1650

(4) NUMBERS.

The abstract substance of the cell: numerical transubstantiations and the radio-war, 1939-1945

'I find it difficult to think of things here', young Alan Hodgkin scribbled on a thin piece of paper at a late hour in March 1940, a grey and cold evening at the Air Ministry Research Establishment at St. Athan. Removed from the tranquil Cambridge, and his usual occupation as an aspiring nerve physiologist, Hodgkin was still getting used to his new life in radar research. 'There isn't much to tell except about my work', he complained to his mother, 'and that is supposed to be very secret. My daily programme is something like this':

> Get up at 7.40 breakfast at 8.00, leave around 8.40 arrive at St. Athan soon after 9.0. Work until 10. Lunch in the officers mess. Work till 6.0 with interval for tea. ... supper at 7.0. Evenings usually are wasted. I made a good resolution that I would try + finish writing up some nerve work and I thought I would be able to do it in the evenings or over the weekends. But so far I haven't managed to do much although I've spent a good deal of time sitting with a piece of paper in front of me.[593]

Despite these frustrations, pieces of paper would get filled in due course. Columns and columns of numbers, data, and equations; Hodgkin's name, in turn, and those of a number of diverted, fellow biologists, notably that of his somewhat junior colleague, Andrew F. Huxley, would become associated with a much more peaceful piece of research - the Hodgkin-Huxley model of the nerve action potential. Seeing public light in 1952, the model became historic almost instantly, celebrated by 1958 as one of the 'brightest chapters of neurophysiology and even biology of all time', terminating an era of 'qualitative mysticism' in matters of understanding the biological cell. It was, unsurprisingly, decorated,

[593] Hodgkin to his mother, undated (c. March 1940), HDGKN A.144

in 1963, with a Nobel prize.[594] There is no question: it shaped conceptions of nervous activity then and ever since. 'To be unkind', one version of its pervasive but barely perceptible impact went, 'one might say it was like giving a Nobel Prize for Literature to people who had advanced knowledge of typewriters, of ink, or perhaps of radio transmission.'[595] It was due to J.Z. Young, who had furnished them with an essential ingredient: the squid giant axon.

The Hodgkin and Huxley model – on first sight, little more than a complicated set of mathematical equations – and its material substrate are the subject of this chapter and the next. There is indeed a significant shift at stake: modeling became a more abstract and mathematized activity. And so for the cell: between 1939 and 1945, as Hodgkin and his future comrades transformed into a different kind of biologist, the cell itself gradually turned into a numerical entity and computational problem. This chapter argues that this transition is best understood not as a radical departure, but by considering how its substrate, the world, itself then was one increasingly and intensely suffused with numbers, quantities, and what I call mundane numerical practices: charts, lists, diagrams, and so on. The next chapter, moving us on from these numerical practices towards less abstract things - electronic technology - will show how this abstract cell would become, or remain, deeply entwined with the things of this newly numerical world – with things new and old: electronic gadgets, cathode ray tubes, feedback control mechanisms, calculation machines, Geiger-counters, ions and radioactive tracers, squids, dissection scissors, and more. This world (and consequently, its biological materials) became, in unprecedented, quantitative detail, empirically resolved, charted and labelled in its remote spatio-temporal dimensions.

The argument: abstract, but mundane

The world we shall explore was still, or even more so, the worlds we know already: worlds

[594] Polyak (eds.) (1957): p.248; Cole (1962): p.113; also see J.Z. Young (1951); nn. (1960); Klemm (1972).
[595] J. Z. Young (1977): p.9.

of synthetics, muscles, electrical things, and medical physics (something often called medical electronics now), even as the import of any one of these domains, relative to the cell's substance, shifted substantially, as we shall see. But the significant difference was, to put the argument plastically, that the world turned more numerical and quantitative now. Artificial membranes, for instance, though their uses increased unabated, were increasingly less defining as regards cell-physiological practice. Similarly for muscle and other ersatz-objects: as much as interwar 'radio culture' faded and was black-boxed into off-the-shelf radios coming in wood-imitate or plastic cases, the generic category of excitable tissues – composed of plants, red blood cells, hearts, muscle, nerve, skin – now gradually decomposed. Discourses of excitability, for reasons well beyond the confines of this investigation, became organized much more definitely around what one heard and read of very often now as the 'most complex and mysterious structure in the universe': not the body, but the human brain.[596]

Circuitry, meanwhile, remained at the heart of the neuro-physiological imagination, though its technological basis differed: no longer hobbyist *bricolage* but the much more disciplined forms of electronic science such as the one Hodgkin was just beginning to internalize as he sat at his desk in March 1940: radar-electronics. Phrased in the language of circuit diagrams, their model, a 'theoretical membrane' in their words, thus looked familiar enough, indeed deceptively familiar – if slightly more complex perhaps:

[596] So the title of a popular book by the science writer John Pfeiffer; see Pfeiffer (1955); some crucial examples include J.Z. Young (1951); J.C. Eccles (1953); Walter (1953a); Ashby (1952); on this rise of the brain, see esp. R. Smith (2001b); Collins (2006); and especially Braslow (1997).

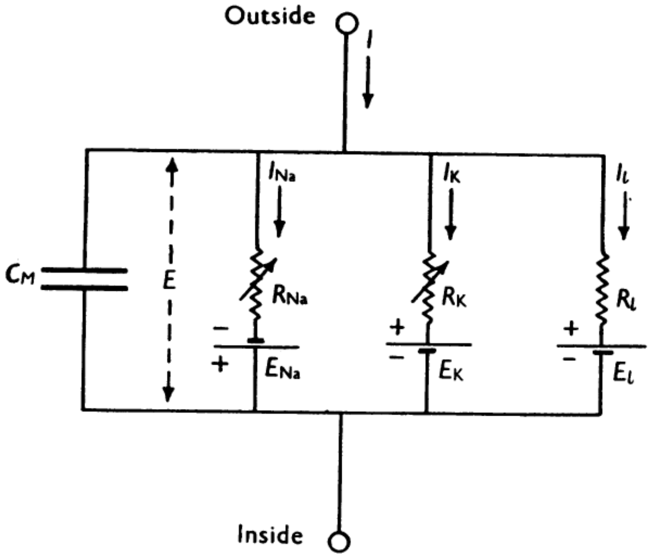

Figure 36: the 'theoretical membrane', 1952

In this diagram one was confronted with a 'reconstruction of nerve behaviour' as Hodgkin and Huxley put it in the famous series of papers that contained the diagram and a set of differential equations, too, which did the formal describing.[597] What one saw depicted on the pages of the *Journal of Physiology* were notably three little, parallel batteries labelled E_{NA}, E_K, and E_l. Each one of them was in series with a resistance, and each one of them was representing a specific ionic current that traversed the membrane during an impulse: 'Na' stood for sodium, 'K' for potassium, 'l' for *leak*. And at its core, their model reproduced exactly this: the temporal dynamics of these individual ionic currents - when fed with the some twenty empirical constants, parameters and subsidiary equations one had constructed, defined, electrically measured, and laboriously cranked through Brunsviga calculation machines.[598]

Here was a notable expression of the world's new numerical substance - something unheard of in the world of physiology: a model of the nerve impulse which was grounded in a wealth of exacting, empirical data, and which exactly reproduced the 'performance of the original system', the giant squid axon, in every detail. The model exactly reproduced,

[597] See especially, the last instalment of the series, A.L. Hodgkin and Huxley (1952).
[598] See esp. 'Discussion' in (1952a): p.51.

that was, the shape, form, and amplitude of the observed, empirical action potential. [599] And although performing these calculations was 'extremely laborious', the very reason for carrying them out, as Hodgkin often explained, was precisely that 'they g[a]ve a definite picture of the sequence of events during the action potential'.[600]

The impulse, for anyone capable of reading the diagram, had ceased to be a simple, atomic event. These equations instead gave a functional portrayal of the bioelectrical micro-dynamics underneath the impulse, everything being based on measurable, definite, physical quantities. When later in the same year, the 'Nerve Impulse' pronged on the November issue of the *Scientific American*, it accordingly was an impulse flickering on an oscilloscope screen: an elegantly swung curve, function-like, superimposed on the regular grid of graph paper: a fundamentally physico-mathematical entity.

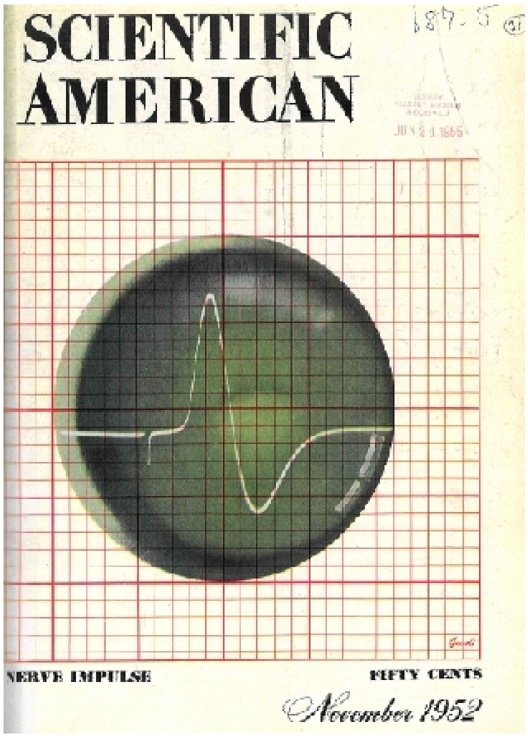

Figure 37: The Nerve Impulse, covering the Scientific American, November 1952

The accompanying article was written by Bernard Katz, yet another radar-veteran and the right-hand man of A.V. Hill. Katz, as we shall see, was also the third man behind the Hodgkin-Huxley model, and he thus authoritatively wrote on the nerve impulse here, that very part of the human nervous system that was now 'fairly well' understood; everything

599 Hodgkin and A.F. Huxley (1952a); and see Pringle, in nn. (1960).
600 Hodgkin, typescript, Cold Spring Harbor Talk (1952), p.16, in HDGKN E.6; and Hodgkin and A.F. Huxley (1952a): p.501.

else, so Katz, was 'still largely a mystery'. A close-up of an intimidatingly huge electronic recording rack underscored the point, having the air of a modern jet-plane cockpit rather than a biological instrument.[601]

The readers of the *Scientific American* were spared the exacting 'quantitative formulation' that this understanding of the nerve impulse had been given. But even to them, it was no longer a mere flickering on physiologists' inscription devices. Nervous activity, as was plainly visible here, had emerged during the 1940s and early 1950s as a highly mathematized, and calculable thing. It was no longer a simple 'alteration', but a composite entity broken down into its various ionic 'component' currents.

For us, a thick, in-depth description Hodgkin and Huxley's trajectories through war-time technology and science will serve to expose the *substantial* ontology of numbers underneath this model of the cell which was indeed unprecedented in its formal and quantitative nature. Together, these chapters thus chart a significant transformation underway in matters of models of the cell. They chart how, in the decades around 1940, such models turned into more abstract, more immaterial, and more formal entities. Hodgkin and Huxley's model is only one (if outstanding) example. But, very much in the spirit of Young's unkind remark above, the ultimate object will be to uncover underneath the seemingly abstract the persistent presence of everyday, and quite mundane materials, technologies and practices. It will require understanding this transformation of modeling practices not as a radical incision, but as an intensification of what went before. These modeling practices were deeply entangled with, or emergent from, the material, everyday world.[602]

As we shall see, there was *systematicity* to biologists being exposed to the kind of 'daily programme' Hodgkin recounted above, and not least therefore, the science and

601 Katz (1952): p.55.

602 In doing so, this chapter converges with those historians who have approached the formal, be it mathematical discipline, information theory, or the history of computing, from the vantage point of concrete materials, instruments, and low-level practices. See esp. Hagemeyer (1979); Mindell (2002); Agar (2003); Warwick (2003); Kline (2004); Grier (2005); Kline (2006); M.W. Jackson (2006).

modeling-strategies they so absorbed (quite evidently) were rather mundane. This includes, but is not nearly exhausted by such laborious calculations as were performed on machines - and with which notably Huxley, himself a prevented physiology student, had gained extensive experience during the war. The next chapter will further show that these programmes can be seen as common experiences. These are biographies typical for their generation of biological scientists, not peculiar and alienating. We shall see how the radio-war meant, in ways that have hardly been appreciated, a large-scale human engineering project in which majorities of the British student population were diverted towards physics and electro-engineering: 'drastic re-orientation', in the words of C.P. Snow, who was crucially involved in culturing these human resources.[603]

It was this systematicity which rendered electronics increasingly banal, an ontology if you will, alongside numbers and numerical practices. Thus the radio-war will feature very prominently in the following - as an agent of *intensification* and *proliferation*. These chapters are to impress us with matters of scale and the mundane, rather than radar's purported high-technology. There is, moreover, a significant historiographical surplus value: in presenting the mundane ontology of the cell around 1940, these chapters substantially challenge the historical narratives of models, modeling and of the nervous system that have hitherto informed our historical understandings of the period. Cybernetics, and thus signals, neural codes, and, in the words of Ralph Gerard, 'Problems Concerning Digital Notions in the Central Nervous System', will play no, or little, role here; even though, that is, we might expect them in an account of the nerve cell at mid-century.[604]

This warrants brief discussion because these registers have been so influential, and because it throws into relief what is meant here by mundane. Gerard above evidently had moved beyond the heat production of peripheral nerve when he now pondered such problems and notions - in connection, as he said, with the 'national fad' of cybernetics.

[603] Snow, 'Hankey Radio Training Scheme', March 1941, LAB 8/873

[604] Gerard (1951); on cybernetics, the standard source is still Heims (1991); also see Pias (ed.) (2004).

Indeed he was himself a member of the famous Macy Conferences on Cybernetics: a 'most provocative' 'group' indeed, Gerard then proudly recorded.[605] As to the cybernetic provocation, there can be no doubt. These registers, or what historians following Lily Kay have diagnosed as the advent of an 'information discourse' which also engulfed the biological sciences, certainly reformatted the contemporary neuro-physiological imagination as well. In the writings of figures such as Gerard's Chicago colleague, the neuro-psychiatrist Warren McCulloch, as Kay influentially had argued, the 'science of mind [then] became a science of signals based on binary logic'. Similar analyses abound.[606]

With some justification the models and visions of nervous behaviour that have shaped our historical understandings of the period are not the ones that were generated from the vantage point of 'practical physics', as A.V. Hill labelled these war-acquired talents of a Hodgkin. Instead it is 'logic' that has informed our accounts of nerve science, and thus the new and provocative, technology-laden 'philosophy of communication' that was beginning to cast its spells over the postwar world.[607] In their famous 1943 paper on 'A logical calculus of the ideas immanent in nervous activity', McCulloch and his youthful assistant, the mathematical prodigy Walter Pitts, accordingly proposed 'to record the behavior of complicated nets [of neurons] in the notation of the symbolic logic of propositions.[608] The "all-or-none" law of nervous activity is sufficient', they argued, 'to insure that the activity of any neuron may be represented as a proposition.'[609]

[605] Gerard (1951).
[606] See esp. Kay (2001): p.592; Hagner (2004): pp.288-294; Hagner (2006): pp.209-216; also see Abraham (2003a); Borck (2005); Piccinini (2004); Gardner (1985); Dupuy (2000); Wheeler, Husbands, and Holland (eds.) (2007); Boden (2006); Christen (2008).
[607] Hill to Gasser, 1 March 1946, AVHL II 5/36; Littauer to Wiener, 23 December 1948, MC22, Folder 87, Box 6
[608] Kay (2001); Abraham (2003b).
[609] McCulloch and W. Pitts (1943): p.117.

Needless to say, McCulloch and his young collaborator here were interested in something different than merely neurons; certainly not, their fundamental bio-physics.[610] Theirs was a deeply meta-physical enterprise. It was certainly perceived in such terms, much more so than historians have cared to acknowledge. 'McCulloch is coming to this country in September', as the British cybernetics missionary Grey Walter noted, for instance, sometime in 1949, and '[h]e has just sent me a stack of MSs entitled variously: Why the mind is in the head/ On half the Extra Pyramidal System/ Finality and form in Nervous Activity/ Through the den of the Metaphysician/ And so forth. They are all rather similar, being lectures to a variety of learned bodies but are full of stimulating phrases and half finished experiments.'[611]

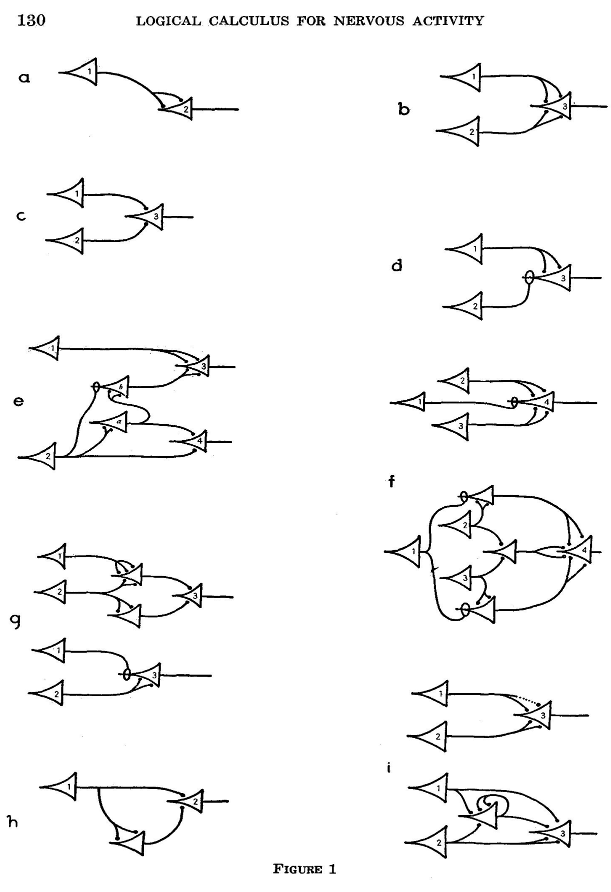

Figure 38: The logical calculus of immanent ideas.

Or, consider the 'highbrow résumé' of the six-part BBC series on 'Communication' broadcast the next year, starring the Bristol neurologist and cybernetic missionary Grey Walter. It might have served as the accompanying booklet to this discourse. Grey Walter's

[610] Ibid., p.131.
[611] Grey Walter to Bates, 28 July 1949, BATES, B.1

briefing was 'provocation … rather than mere instruction or absolute scientific integrity.' The series accordingly was to provide the target-audience - of 'average, not exceptional intelligence' - with 'synoptic glimpses' (hence many models, analogies and other 'illustrations') of 'the way information is conveyed from one creature to another'. The series began with 'Noise' and proceeded via 'Signals, Codes and Ciphers' and 'TV and radar, automatic devices' to the grand finale: the 'Nervous System - analogies and differences'.[612]

This discourse, in other words, was real enough, and as such, part of the very transformation the remainders of this thesis engage with. Here I can only gesture at how, as historians of science, we have by and large failed to interrogate its historical realities when mobilizing it to frame our narratives. It is, in part, the fact that such symbiotic relations as the one between Grey Walter and the BBC were by no means exceptional, which renders this discourse highly problematic as an historical account of technological evolution. It cannot simply serve to contextualize the local stories we tell. By the same token, it is not very illuminating as a guide to the mundane and less stimulating world of the nerve physiological laboratory. The likes of MRC secretary Sir Eric Mellanby took the position that there was little worthy of note (or, for that matter, support) to such approaches: People 'speculating along such lines have often hesitated putting pen to paper. Their reason is often because they have no adequate data either to check or support their speculations.' [613]

It is not least therefore that the following takes a very different, deliberately unspectacular perspective on this world. We need to think, I argue, of electronic technology and numerical practices and the ways that they began to shape the biological sciences in less futuristic and more modest terms.[614] For the physiological mainstream, it

612 'Draft outline of suggested six talks', File 'Rcont 1 William Grey Walter, 1948-1962', BBC Archives
613 See letter Mellanby (MRC) to Randall, 29 March 1949, RNDL 2/2/1
614 In this, I converge with a long line of historians of technology whose work deflated the cybernetic incision story. See Hagemeyer (1979); Noble (1986); Mindell (2002); William Thomas (2007); Kline (2009); as a story of war-time science, it is indebted, moreover, to Edgerton (2006b).

was 'such men' as Hodgkin who were fortunately 'already busy trying to find the basic facts' on which any such speculations might eventually be built.[615]

This basic business has been obscured from our view, and one reason, ironically, are the complex entanglements of the cybernetic vision with its own popularity. Thus, 'detailed quantitative experimental programme[s]' such as the one on a 'rigorous description of the time-course of the spike potential' of a single axon which notably Norbert Wiener in fact *did* enthusiastically cook up together with the Mexican electro-physiologist Arturo Rosenblueth (and the aid of the Rockefeller foundation) quite definitely did not mesh with the public role as chief 'Philosoph[er] of Communication' that Wiener was to assume.[616] It was rather similar in spirit to the 'theoretical membrane' issuing from the hands of Hodgkin and Huxley. But, Wiener's cybernetic allies did not necessarily find such matters worthy of discussion, as Wiener learnt when their parallel electro-physiological efforts concerning a quantitative, rigorous 'study of [heart] flutter and fibrillation' weren't admitted to the programme – despite Wiener's insistence as to their importance 'for the purposes of our conference'.[617]

One had to keep in mind ways of reaching out that 'might permit broad public understanding and appreciation,' as Wiener frequently was advised:[618] 'channel[s]' that 'would make the implications of CYBERNETICS amenable to presentation in dramatic and concrete terms with meaning for the average man'.[619] By then, Wiener's *Cybernetics* had sold a spectacular 13,931 copies, with another 5,000 copies waiting to be printed and a more accessible version in commission. *The Human Use of Human Beings* hit the shelves in

615 Ibid.
616 This was a quite common identification; cited is Littauer to Wiener, 23 December 1948, MC122, Box 6, Folder 87
617 Wiener to Fremont-Smith, 25 April 1946, MC22, Box 5, Folder 70; and Rockefeller Foundation to Wiener, 29 May 1946, MC22, Box 5, Folder 71
618 Jones to Wiener, 17 November 1948, MC22, Box 6, Folder 86 and see especially Wiener (1950).
619 Ibid., also see Wiener to Pfeiffer, 29 May 1948, MC22, Box 5, Folder 83; Ehrlich Smith to Wiener, 2 December 1948, MC22, Box 6, Folder 87; McCulloch to Rich, 14 April 1949, McCulloch papers, Folder 'AAAS'; McCulloch correspondence with Pfeiffer, Folder 'Pfeiffer, John E.'; and see File 'Prof. J.Z. Young, Talks 1946-1959', BBC

1950, without, needless to say, much discussion of heart flutter.[620]

As a techno-scientific tale of the nervous system and its models the homogeneous amalgam of electronic brains, cyborg sciences and information discourse is fraught with difficulties. It is not simply the case that the historical narratives of signals, codes and digital principles tell only part of story - this much would be trivial. It is the very historical-technological 'context' they invoke which is historically problematic. In the laboratory, as we shall see, the impulse was never digital, off/on: it was hundreds and hundreds of measurements, calculations, calibrations, interventions and observations. And as far as most people - and certainly most biologists - were concerned, it was not the advanced radar-predictors and esoteric time-series of a Norbert Wiener that would come to define the 'ontology' of this new world which Peter Galison has advanced in this connection.[621]

More banal than even Hodgkin's programme and certainly truer to the humble day-to-day grind of radar science, the case will be made that it is the trajectories of the 'Two Biologists [who] Went to War' and who anonymously reported of their experiences in a 1952 issue of *Discovery* which should inform our accounts. 'Case-Book no.1' here used the occasion to air his continual frustration of *not* being made proper use of, of being allocated, seemingly randomly, to serve as a truck driver, photo interpreter, squadron officer boy, poster artist, heavy labourer in a bomb dump and stock-control clerk: 'eventually they posted me on a ten-and-a-half months' course of training for the trade of a wireless mechanic – a subject of which I knew nothing and cared less.' For case-book no.2, it too was decided that 'he should be an electrician'.[622]

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620 Technology press to Wiener, 26 October 1949, MC22, Box 6, Folder 104; Brooks to Wiener, 10 November 1949, MC22, Box 6, Folder 106

621 See esp. Galison (1994); also see Pickering (1995); Edwards (1997).

622 nn. (1952b).

Case-book Hodgkin: missing agents, 1939

Plymouth, Devon. Summer, sun, 1939. The world was waiting for another war. 'I am waiting now for squids', twenty-five year old Alan Hodgkin impatiently wrote in July, 'which so far have not been coming in very well'.[623] Fortunately enough, the squid-situation at least soon was improving, and it will give us an opportunity to properly introduce the proponents of this story: The giant axon, Hodgkin and his new assistant Andrew Huxley, then a final year Natural Sciences Tripos student reading physics, chemistry and physiology – this summer, he revealed himself as 'a wizard with scientific apparatus'.[624] By August, one was busy experimenting, and their 'exciting experiment' would, 'if it comes off ... be the most important thing I've ever done', or so Hodgkin informed his mother, in easily understandable language:

> This is to get a wire inside the giant nerve fibre and record nervous messages from inside instead of obtaining them from outside as everyone has done up till now. The experiment worked perfectly the second time we tried and I can see no reasons why it shouldn't work again. So we're both very excited.[625]

Exciting, as we shall see, it was. Hodgkin just recently had returned from America, where, aided by a Rockefeller Stipend to 'spend his time with Dr. Gasser at the Rockefeller Institute', he was to familiarize himself with the methods of American workers in neurophysiology and biophysics.[626] The years 1937-1938 had proved something of a revelation for Hodgkin indeed: Hodgkin then had been introduced to the subtleties of electronic recording gadgetry by Jan F. Toennies, a trained electrical engineer of the kind we know. Before arriving at Gasser's laboratories, he had passed through the Siemens Zentral-Laboratorium already, and the Kaiser-Wilhelms-Institut für Hirnforschung too:

623 Hodgkin to his mother, 11 July 1939, HDGKN A.142
624 Hodgkin to his mother, 23 August 1939, HDGKN A.142
625 Hodgkin to his mother, 13 August 1939, HDGKN A.142
626 Extract letter O'Brien to Mellanby, 18 February 1937, FD 1/2627

Forgetting about 'radiation fields and other irrelevant ideas', in Gasser's lab Hodgkin was taught *physical sense* instead- 'to think only in terms of electrical leaks, stray capacities, and actual spread of current in the tissue.'[627] His path then also crossed that of Kenneth Cole who personally initiated Hodgkin to the secrets of high-frequency measurement as they worked together on the electrical properties of the squid giant axon during the summer at Woods Hole.[628]

Hodgkin wasn't a newcomer, then, to the biophysics of nerve as he was released from active service at the Telecommunications Research Establishment (TRE) in Malvern some seven years later, in April 1945. Far from it. But neither, as we also shall see in this section, had the undisturbed, pre-war world yet been entirely prepared for the puzzling discovery he and Huxley had been making in the late summer of 1939. It would be the reference point for everything to follow.

Trained in Cambridge under the tutelage of William Roughton, having listened ardently to the lectures of colloid scientist Eric Rideal, having spent summers in A.V. Hill's little bungalow near the Plymouth Marine Biological Station, the story of Hodgkin's scientific socialization in the 1930s reads like the reflection, in the cloistered, academic Cambridge, of the story so far.[629] Like Hill thirty years before him, Hodgkin and Huxley were products of the Natural Sciences Tripos, even if this wasn't quite the same Cambridge any longer. Their generation was the first to enjoy the new opportunities Cambridge then began to offer aspiring biological scientists. Thanks largely to a major benefaction of Rockefeller Foundation in 1928, considerable expansions - laboratories, buildings, staff - were underway notably in biochemistry, physical chemistry, experimental zoology, general and nerve physiology, biophysics and colloid science.[630]

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627 Hodgkin (1992): esp. p.71.

628 Cole and Hodgkin (1939).

629 A very detailed, but historically narrow account can be found in Hodgkin's autobiography. Hodgkin (1992).

630 Cambridge University Reporter, 1928-29, p. 162; on the Rockefeller Scheme, see Kohler (1991): pp.182-

Unlike their physiological peers emerging at the time from other universities and medical schools, there was no anatomy, no pathology, no histology to be found on their timetables. Instead it would be subjects such as physical chemistry, physics, advanced biochemistry, and long hours of laboratory classes: 'the hard discipline of a proper training in classical physiology', as A.V. Hill knew, that could only be had in Cambridge.[631] Bryan Matthews, who we will remember as a wireless jack-of-all-trades, then first instituted an 'electronic kindergarten' through which physiology students were sent 'before being allowed to work with ready-made recording apparatus'; it was the do-it-yourself ideal put to pedagogical effect.[632] And there had been major reforms underway concerning the Tripos at large with the view to pre-empting students from specializing too narrowly in either physical or biological subjects. 'Much of the present research is on the border line of two or more subjects' these Tripos reformers believed. It was essential therefore not to 'stereotype the various divisions of the Natural Sciences'.[633]

These reformers we already know: Fletcher, Hill, Barcroft, Rideal, Roughton, and notably Sir William Hardy, biophysicist and director of the Food Investigation Board, all had their hands in these reforms. They were a reflection not only of Cambridge's uniqueness or the generous foresight of the Rockefeller Foundation, but of the forces which had shaped their own biological borderland projects. They shook up Cambridge and the British biological world generally:[634] The 'new and highly technical' methods in medicine, the needs of the Empire, in agriculture, fisheries and the food industry called for the 'broadly trained' 'kind of biologist', as Hardy had submitted in this connection, whose education didn't map on the 'merely historical' academic classifications.[635] An 'economic

188.

631 Hill to Fletcher, 7 May 1929, FD 1/1949

632 Donaldson (1958): foreword.

633 Minutes 9 February 1933; Saunders to Priestley, 8 February 1933, CUL/University/Min.VII.18; also see Kohler (1991); Weatherall (2000); Chadarevian (2002).

634 Stadler (2006).

635 'What is a biologist?' (memorandum, November 1930), CAB 58/162; and Dean, 'A review of the medical curriculum' (1930), ROUGHTON/APS, Box 34.60u

biology job ... would probably only result in more profit going into some capitalist lands instead of to the good of the Society as a whole' Hodgkin, meanwhile, resolved for himself in 1933, and 'this depression' being in full swing, he was at any rate soon gravitating towards the more prestigious problems of physiology: nerve.[636]

Hodgkin, however, had learned his borderland lessons well. Biology was full of 'many very interesting things', as Hodgkin confided as an undergraduate, but 'the Science as a whole is and probably always will be complicated ~~business~~ and rather a muddled one.'[637] Hodgkin accordingly opted for physiology in part II of the Tripos which was a far less muddled affair. He soon was consumed by advanced lectures, notably, in physical chemistry, difficult subject matter taking up 'about twice the amount of time theoretically allotted'.[638] The fundamental outlook he acquired still as a student was displayed in 1935, in a discourse on a 'Mathematical Theory of Nerve Conduction' before the Cambridge Natural Science Club. Hodgkin there reviewed the ways the surface of a nerve fibre could be 'represented' by a chain of condensers – an 'Electrical Model'.

What Hodgkin's diagram does not reveal is just how well versed Hodgkin was in the latest advances into the biophysics of excitability: Cole, Osterhout, Hill, Rideal, and Donnan - these were the names accompanying Hodgkin in those days.[639]

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636 Hodgkin to his mother, March 1933, HDGKN A.126
637 Hodgkin to his mother, letters July 1933, HDGKN A.127
638 Hodgkin to his mother, letter '2' autumn 1933, HDGKN A.128
639 'Mathematical Theory' (1935), HDGKN A.60

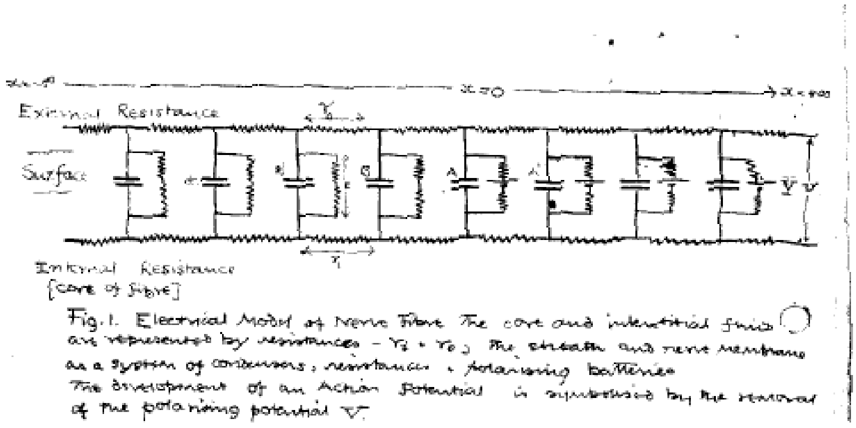

Figure 39: 'Electrical Model of Nerve Fibre', 1935 (drawing by Hodgkin)

Hodgkin, evidently enough, was well prepared by the time he arrived in America. By then, the squid was already entering its third season as a 'preparation' at Woods Hole, coming under the purview of a growing number of investigators.[640] With the *Nitella* algae as their 'understudy', not least Cole and Curtis had made steady progress with their impedance measurements of membrane changes during an impulse. In fact, this *change* had revealed itself surprisingly complex.

At the time, the received doctrine, the so-called membrane theory, suggested that the membrane would simply and 'practically disappear electrically' during nervous activity, a deeply ingrained notion that seemed well justified empirically, notably by high-frequency studies on erythrocytes and marine eggs.[641] Cole and Curtis, naturally enough, operated

[640] E.g. Bear, Schmitt, and J. Z. Young (1937); Schmitt (1990): pp.100-102.
[641] Miles (1972); also see Adrian (1932a): pp.16-21; A.V. Hill (1932a): p.12; Gasser (1933): p.143; Davson and

under the intuitive assumption of a sudden membrane 'breakdown' when they turned to *Nitella*. Initially the data so produced proved vexingly confused. Reluctantly, Cole and Curtis came to appreciate that *Nitella* behaved differently. In this algae, the 'capacity' of the membrane remained 'essentially unaltered' - even during activity. This realization broke the spell, and confusion quickly gave way to pattern. From the impedance characteristics, and some electro-engineering analysis, it was possible to infer the changes in another property - *conductance* – that the membrane underwent after all. This, it turned out, increased some thirty to two-hundred fold as the membrane turned 'active'.[642]

When, in the spring of 1938, Cole and Curtis were able to 'essentially duplicate' these experiments with squid axons at Woods Hole, 'quite unannounced' a young Englishman 'popped in during an experiment'.[643] The Englishman was, of course, Hodgkin who very eagerly embraced what he saw. Hodgkin returned to Cambridge in late 1938 and, new equipment in tow, resumed his job as a demonstrator in physiology. Among his students that fall was Huxley, and the next summer, Hodgkin took him on as an assistant for investigations to be carried out in Plymouth: Inserting an electrode into the - giant – axon.

This was now an obvious, if not entirely non-trivial next step. A year earlier, for instance, Hodgkin's illustrious fellow student and friend Victor (Lord) Rothschild, had availed himself of microelectrodes – glass pipettes - and the corresponding micromanipulation-techniques to elucidate the 'Biophysics of the Egg Surface of Echinus Esculentus' by 'intracellular' means, which is to say *across* the surface of the egg.[644]

The squid giant axon, we know already, made similar interventions imaginable. Being a more 'active' electrical object, however, the axon posed many additional complications when it came to pushing electrodes into this delicate structure. Hodgkin and

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Danielli (1943): preface.

642 Report of Research aided by Rockefeller Foundation Grant RF 36160, 1938, RF RGII 200D, Box 133, Folder 1650; and see Miles (1972).

643 Miles (1972); also see Hodgkin (1992): pp.95-96; and pp.115-116.

644 Rothschild (1938).

Huxley managed by inserting - by 'means of system of mirrors and a microscope' – a coated silver wire stuck in a 200 μ glass tube filled with sea-water. This did the trick, eliminating polarization effects and not obviously inflicting damage onto the axon.[645]

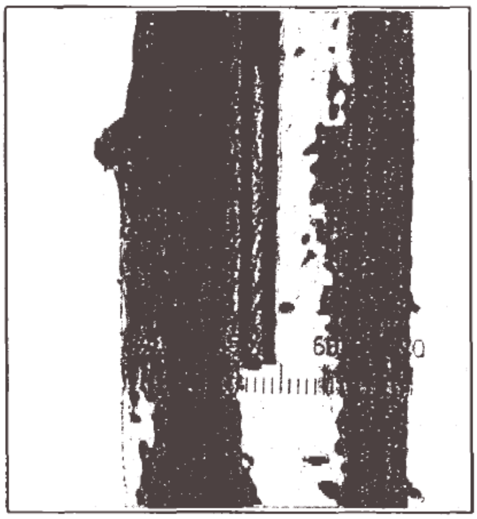

Fig. 1.
PHOTOMICROGRAPH OF ELECTRODE INSIDE GIANT AXON. 1 SCALE DIVISION = 33 μ.

Figure 40: 'the most important thing I've ever done', Inserted electrode, 1939

The two of them eventually succeeded in measuring action potentials between the interior of the fibre and the external medium in the late summer of 1939. '[O]ne feels a bit in an ivory tower doing abstract scientific experiments in the present time', Hodgkin admitted, but the results were astonishing indeed.[646] At a resting potential of about 50 millivolts, the absolute magnitude of the action potential revealed itself at 90, thus 'overshooting' its expected value by some 40 millivolts. Expected, that was, on the grounds of the membrane theory. According to this, the potential should have been simply reduced to zero as the membrane broke down; and not, as was observed, undergo a significant 'reversal'.

645 Hodgkin and A.F. Huxley (1939).
646 Hodgkin to his mother, 23 August 1939, HDGKN A.142

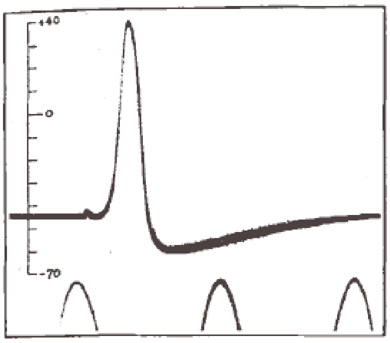

Fig. 2.
ACTION POTENTIAL RECORDED BETWEEN INSIDE AND OUTSIDE OF AXON. TIME MARKER, 500 CYCLES/SEC. THE VERTICAL SCALE INDICATES THE POTENTIAL OF THE INTERNAL ELECTRODE IN MILLIVOLTS, THE SEA WATER OUTSIDE BEING TAKEN AT ZERO POTENTIAL.

Figure 41: The 'overshoot'

By then, of course, the concept of a simple 'breakdown' had already fissured in the hands of Cole and Curtis. But a reversal of the potential seemed to fit into this picture even less: 'Things look[ed] pretty bad', Hodgkin resolved, 'for any theory of this type.'[647]

Without further commentary, these observations were published in a short communication in *Nature* in late October. In private, the 'resting potential action potential problem' was pondered: 'why action potential bigger than resting potential' [sic], Hodgkin jotted down in his notes. And: what were the 'possible reasons'?[648]

The various reasons Hodgkin considered harked back, most unsurprisingly, to ions – or, their tangible appearance, salts - those omnipresent agents of bioelectricity, life, nutrition, osmotic balance and more. More readily determined than the fleeting action potential, resting potentials in particular had long become closely - and causally - linked to the potassium-imbalance characteristic of (most) biological cells. A.V. Hill's widely influential *Chemical Wave Transmission in Nerve* (1932), for instance, had made a strong case for the 'peculiar' 'effects' of potassium ions. 'The K', it was known, was far more concentrated inside the cell than in the exterior fluid. Variations of the external potassium concentration had striking effects on the magnitude of the resting potential, and there was accumulating evidence too that potassium 'escape[d]' during stimulation: 'It seem[ed],

[647] HDGKN D.96, notes 'Islay, July 1939'
[648] Ibid.

therefore, that the surface is rendered permeable during activity', as Hill ventured. These 'facts appear[ed] simple' enough.[649]

A mere 'escape' of potassium, however, wasn't sufficient to account for the reversal of the potential, as Hodgkin almost instantly realized. No longer did the facts appear simple enough. The various scenarios Hodgkin began to consider thus brought into the picture an entire range of additional ionic species - calcium, magnesium, chloride, sodium and some more complex, polyvalent species as well. For a physiologist, this was a natural reaction. The pervasive presence of ions in connection with everything physiological, gauged with such simple and inconspicuous tools as ph-indicators or potentiometers, was palpable everywhere from lactate ions in fatigue to the Ringer-solutions physiologists' bathed their preparations in. Indeed, in physiological terms, ions were existing in the first instance, palpably and qualitatively, as their own potent effects. Ions were *agents* whose potency became manifest through tissue alterations, the loosening of membrane structures, swelling, shrinking, cellular narcosis, the extinction of excitability. Potassium, especially, had well known immediate potent 'effects' on excitable tissues. So had rubidium, and somewhat less instantly, lithium, ammonium, caesium, magnesium, barium, calcium, and a plethora of more complex 'salts' as well.[650]

Within a short few years, this situation would shift entirely, as we shall see. With the explosive career of radio-active tracer elements in the aftermath of WWII, substance exchanges, permeation, diffusion, secretion, 'fluxes', and 'transport' resolved into novel spatio-temporal dimensions, and they left behind them trails of quantitative data. But in 1939, this biophysical microcosm was still opaque. '[A]uthoritative figures' on the 'ultimate [ionic] composition of biological material' were hard to come by, as D.A. Webb, a Plymouth-based marine scientist well-versed in 'micro-estimation' methods complained.

[649] A.V. Hill (1932a): pp.30-35.
[650] E.g. Schaefer (1942): esp. pp.26-29; Höber (1946): pp.383-389; Gallego and Lorente de Nó (1947); Fenn (1949).

And even less ultimate and authoritative ones were scarce, providing a very slim basis indeed for the diffusion equations, the 'theoretical potentials', Hodgkin began toying around with in considering which, if any, combination of ionic displacements would produce the desired effect: the overshoot.[651]

A first systematic foray into assaying the electrolytic contents of the axon's interior which J.Z. Young, Hodgkin himself and Webb above were still undertaking in late 1939 did little to advance the situation.[652] And it was not only the low resolution of the world which meant obstacles to the imagination. The complications introduced by the potential *reversal* seemed to call - at the very least - for additional 'agents' so as to account for the 'puzzling' results. It called for a more complex picture of nervous action, in short, and in ways that considerably complicated the computing of 'theoretical potentials' from ionic composition data.

One was left with 'as yet unknown agencies' or some 'missing' factors and a discrepancy of some 10mV relative to average action potential values – the overshoot.[653] This was the impulse at 1939: a suddenly slightly anomalous phenomenon that did not fit the intuitive picture of a simple membrane breakdown any longer. Neither was there much room, or time, in this world for speculation. From the perspective of ions and their agency, it was a largely qualitative one, more difficult to compute, its ultimate composition obscure; Hodgkin and Huxley returned to Cambridge on August 31: 'No one here seems to know what they are going to do in the war', Hodgkin made out, 'and I am in the same position.'[654] Some three weeks later, Hodgkin found himself 'living in small hut in the country', in convenient distance to the Royal Aeronautical Research Establishment in Farnborough.[655] Four months later, he was re-allocated to St. Athan, South Wales, home of Airborne Radar

[651] Webb (1939): p.178; Webb and Fearon (1937) also see 'Note on the resting potential action potential problem' (1939), HDGKN D.96.
[652] J. Z. Young and Webb (1940).
[653] Ibid., pp.308-309.
[654] Letter to mother, 31 August 1939, HDGKN A.142
[655] Undated letter Hodgkin to his mother, late September 1939, HDGKN A.143

Group 12.

Radio War

For the next almost six years, the reversal 'problem' was largely put to rest. Across the Atlantic, investigations initially continued, Cole and Curtis stumbling over the overshoot as well. They too would be diverted soon – a 'four year black-out', said Cole; 'all this seems another world now,' or so went Hodgkin's response to Cole's 'rather similar experiments' in late 1939.[656] Like many another academic scientist, Hodgkin was already busy assimilating himself to a different world. They adopted more fluid and less disciplinary identities, embraced - or had to embrace - a to them unfamiliar kind of engineering science, and made contact with the forefronts of a rapidly transforming electronic technology: radar.

'Nearly all found difficulty in adapting themselves to the atmosphere of Government research', A.P. Rowe, wartime superintendent of Britain's foremost radar establishment, the Telecommunications Research Establishment (TRE), wrote in his *One Story of Radar* (1948), 'but, as years went on, ... University scientists came gradually to understand that a laboratory effect was not enough; that it was but the beginning of the long road to the production of a device usable by the R.A.F.'[657] Radar veterans, meanwhile, were more prone to idealize the experience. 'TRE was a unique institution … where the problems of the week were thrashed out in discussions so democratic that the humblest lab technician had no scruples of telling a Nobel laureate that he was talking nonsense', as radar-scientist-turned novelist T.C. Clarke had one of his fictional characters, Schuster, exclaim.[658] Reminiscing in somewhat less rosy terms, Cambridge zoologist Pringle, yet another case of being diverted, celebrated scientists' coming to appreciate the values of

[656] Miles (1972) and Undated letter Hodgkin to his mother, c. autumn 1939, HDGKN A.143.
[657] Rowe (1948) quoted in Pringle and Peters (1975): p.544.
[658] A.C. Clarke (1970): p.116; also see esp. Latham and Stobbs (eds.) (1999).

‘organized’ team-work, co-operation and the effectiveness of, in his words, ‘empirical applied science’, or: ‘trial-and-error methods in the hope of achieving quick results.’ All this, was in contrast to ‘the intentionally individual atmosphere of research in a university department’.[659]

Here, gradually, as Pringle had reminisced elsewhere, one witnessed a ‘tradition [that] arose, and grew, until it became almost second nature to … TRE staff’.[660] The following is concerned with exactly this second nature, and in many ways, this will be a familiar story of war-time science. As Charles Thorpe has argued in this connection, this second nature meant not least a mentality dictated by the organizational and temporal logic of large-scale enterprises rather than the pace of university science.[661] For its inhabitants, especially those who felt their curiosity stifled, places like TRE seemed like an ‘enclosure’ for ‘specialists working as automatons’ and not a ‘facility for thinking’, as Manchester physicist Bernard Lovell, whose team Hodgkin had joined, diagnosed in 1944. TRE was ‘a place where telephones [rang] continuously, where one comes in not later than 0900 and leaves not earlier than 1900 hrs. It [was], quite rightly, a place where all priorities and interests [were] centred around next week’s operations’.[662]

In itself this would have reinforced a more narrow, technical, vision of their doings; here cities and people turned into blips on radar screens and data on the ‘operational performance’ of their laboratory effects. There was, it sounds familiar enough, ‘no question that this was a technological war’, as *Combat Scientists* (1947) confidently declared; also, as Pringle put it much later, in 1975, this was not a ‘biologists’ war’.[663] But when, in the following, we begin to chart this second nature and the emergent, numerical ontology of the cell, these familiar-sounding stories of war-time science will be put to less familiar ends. The typical emphases on features such as team-work, co-operation, and mission-

[659] Pringle and Peters (1975): pp. 542-544.
[660] Pringle, The work of TRE in the invasion of Europe (MS, c.1945), p.2, PRINGLE
[661] Thorpe (2004).
[662] ‘Plan B’, Memorandum 20 April 1944, copy in BL 7/1
[663] Theismeyer, Burchard, and Waterman (1947): p.127; Pringle and Peters (1975): p.538.

orientation, for instance, will recede into the background on this account; neither will we be particularly concerned with the radio-war as a source of technological novelty or site of high-tech war.

Instead, to throw into relief the transubstantiation of the cell, we will have to follow our actors into the less well charted, humble and everyday details of their refashioned lives amidst electronic stuff. In terms of the nerve cell, Hodgkin and his friends and colleagues already were, evidently enough, on a trajectory centring on ‘electrical models’ and a good deal of physical chemistry - ions - as well. But still, the concrete and material meanings of the terms involved would subtly shift, appearing differently in the light of what they learnt and saw. More generally, these physiologists’ sense of quantitative and theoretical approaches was confronted with quite different realities – particularly that bestowed on numbers.

This account from the ground shall focus on Hodgkin, in part, because we can draw on much material in his case, both archival and, owing to his autobiographically prolific war-time colleagues, published.[664] But others recruited from the small circle of biophysical colleagues who would make up Hodgkin’s post-war ‘team’ of investigators will also figure prominently. Huxley apart, their conversion experiences are only touched upon here. They would have been similar. Among them were Bernard Katz, A.V. Hill’s son David and Richard Keynes, a nephew of Hill’s, whose Tripos degree course was switched from physics, chemistry and physiology to ‘advanced physics’ to prepare him for his eventual work in ‘radar research’ at the Admiralty Signals Establishment, Surrey. ‘A sound practical sense’, Hodgkin approvingly surmised of his future PhD student, ‘of the difficulties of research and the way it should be planned’ belonged to the resulting virtues.[665]

Together these future model-makers shared a biographical trajectory through radar,

[664] The circle of Hodgkin's close colleagues pretty much exhausts what there has been written along these lines, in addition to Hodgkin (1992); see Lovell (1991); Hanbury Brown (1991); Bowen (1998).

[665] On Keynes, see ‘Report on qualifications’ (nd) in HDGKN, H.28. Keynes entered Trinity College in 1938, left in 1940, and returned in October 1945 to study for the NST, part II in physiology.

operational research, and gunnery control: Within months, Hodgkin found himself immersed in the problems of centimetre-radar at TRE. The somewhat less senior Hill, Huxley, and Keynes were rushed through their final years of studies, capped off with a special emphasis on physics. In due course, Hill and Huxley re-surfaced as members of Patrick Blackett's 'circus' of fame – 'operational researchers' - busy adapting radar to the problems of fire-control. Katz, even more peripheral to any physiological laboratory, was 'fixing radio stations in New Guinea' before he moved on to the Radio Physics Laboratory, Sydney.[666] We will eventually supplement these few and privileged perspectives, but for now, they can stand as descriptive guides as we enter the world of radar, so as to convey, in the words of the TRE *Teaching Panel*, something of 'the atmosphere of TRE'.[667] 'If good biologists and chemists can be got', as one of its members said, 'let us use them.'[668]

***

Junior Scientific Officer Hodgkin joined the airborne radar group at St. Athan, South Wales, in February 1940. Only recently, the entire establishment had been evacuated from its original site on the Southern coast of England. In yet another upheaval of establishment life, within months, the group would have to move again; this time, to Malvern, Dorset, where TRE would take over Malvern College, a boys' school until the outbreak of the war. 'T.R.E.', as W.B. Lewis, the future superintendent of the establishment, enthused in 1945, now grew into 'an organism of artists in applied electronic science'.[669]

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[666] Katz, 'Curriculum Vitae', dated 29 March 1945, copy in AVHL II 4/47
[667] TRE Teaching Panel, record of 3rd meeting (15 March 1944), BL 7.1
[668] 'University Radio Syllabus 1942-43', Report April 13 1943, LAB 8/506
[669] Lewis, *The Role of T.R.E. in the National Scientific Effort* (MS), October 1945, AVIA 15/2260

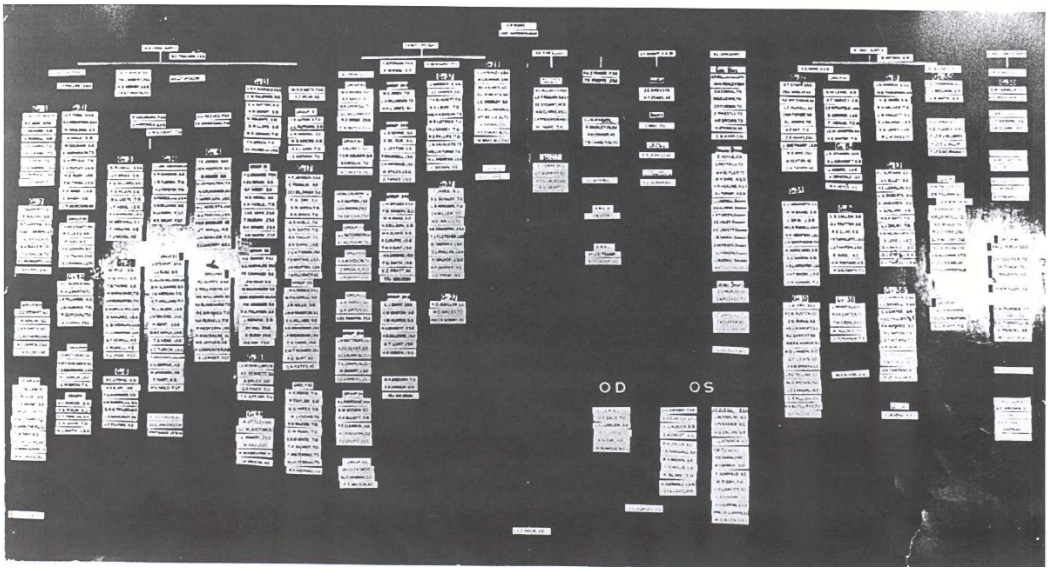


Figure 42: TRE organizational chart, c.1943

For Hodgkin, like many another, becoming such an artist meant the initiation to a different form of scientific life; less academic, less discipline bound, and far more hectic. At its peak, TRE alone meant home to some 830 technical and scientific officers, 430 'industrials', 310 men employed in the drawing offices, and a small army of clerical, administrative and 'ancillary' staff: 4.000 men and women in total.[670] 'If the radar stations he had known were villages', *Glide Path*'s fictional hero Alan told himself, '*this* was a city'.[671] Complete with cinema, library, a radar school, a visitor Hotel, weekend dances, nearby pubs, and countless barracks, hangars, workshops and laboratory buildings, TRE comprised some 40 research and development groups and sprawled out over a considerable territory. Directed by Chief Superintendent A.P. Rowe, it was a generally male environment: '[A]bout 80 per cent of the people being men, and also about the same percentage under 35'. Clearly, this was 'not an average community'.[672]

Air raid precaution and civil defence exercises and sudden and frequent relocations - of laboratories and entire research groups - brought 'confusion in all our work', as for

[670] See files in AVIA 15/3820; AVIA 15/2260

[671] A.C. Clarke (1970): p.29; also see the many anecdotes collected in Latham and Stobbs (eds.) (1999).

[672] 'Welfare - ...Complaints and Suggestions', memorandum (nd), BL 7.2

one, Hodgkin recorded in frustration.[673] Food too, of 'vital importance to ... people whose work calls for more than the usual amount of nervous energy', was monotonous and varied little: 'more fruit and a greater variety of puddings' were sorely missed, as were '<u>balanced</u> vegetarian dishes' or the 'occasional savouries'.[674] A 1943 'census' found majorities among TRE staff 'dissatisfied' with present living conditions and still in 1945, an inquiry unearthed 'several hundred hardship cases'.[675] 'Digs' were usually shared, leaving few spaces of privacy and little escape from the daily grind. Left with 'very little energy' after long days of work, doing 'something constructive in the evening' often was difficult if not 'depressing', as Hodgkin soon discovered: 'we don't seem to do much else besides work and listen to the radio': 'Sometimes days and weeks slip by and you hardly notice they are gone.'[676]

It was an intense experience, and a large-scale development and engineering enterprise that Hodgkin was drawn into - the development of a principle. Keynes' superior, Dr. E.S.C. Megaw, Chief Scientist at the Admiralty Signals Establishment, summed up the 'primary characteristics' of this 'new technique' thus

> Firstly it is necessary to know that something is there, ...; secondly it is necessary to know where there is, with adequate accuracy and continuity; and thirdly, it is necessary to be able to distinguish wanted responses from one another and from unwanted ones, either natural or man-made, with adequate speed and certainty.[677]

It might have come from a laboratory manual on electrophysiology. Radar – *RAdio Detection and Ranging* – was, no doubt, a high-tech means of electronic observation. Its development had been underway since the mid-1930s. A.V. Hill indeed was one of figures involved in supervising the effort (the capacity he is far better remembered for than his biology).[678]

Hodgkin initially was assigned to a group of engineers around Manchester physicist

673 Hodgkin to his mother, 5 May 1942, HDGKN A.148
674 'Welfare - ...Complaints and Suggestions', memorandum (nd), BL 7.2
675 'Census of living arrangements', 6 January 1943, Lovell papers BL 7.2; Air Supply Board 'Note by C.E.E.', 4 December 1945, AIR 20/3850
676 Quoted are letters Hodgkin to his mother, undated (1940), in HDGKN A.144; 6 October 1940, A.145; and 29 January 1941, A.146
677 Megaw, 'New Techniques', Secret memorandum 13 June 1946, ADM 220/89
678 E.g. Zimmerman (2001).

Bernard Lovell which was busy with the testing, analysis, and design of wave-guides - radar antennas (on which more later). Already beginning in summer 1939, the airborne group had successively been enlarged with the addition of civilian scientists recruited mostly from the Cambridge and Manchester physics laboratories. By 1941 TRE *Group 12* had grown to some nineteen members, and in the meantime, several other groups and establishments had become involved as well as the laboratories of EMI and GEC.[679] Within a few more months, airborne radar turned into a huge production effort, dispersed among the three services and several research establishments, as well as a growing number of larger and smaller industrial firms.[680]

In the course of 1943, the purer scientific interests were to become strained even further. Early in that year, airborne radar was first introduced, successfully, to operational use in air-raids on German cities.[681] By summer, Hodgkin recorded, 'what is known as a crash programme has been laid on in order to get production at the earliest possible time.'[682] With increasing amounts of data on operational 'performance' pouring back in, the huge network of laboratories, workshops and production facilities began to move. Firms such as Ferranti, Metropolitan-Vickers, The Gramophone Co., Cosmos, Pye Radio, EMI and a plethora of smaller sub-contractors churned out displays, spark gaps, klystrons, Perspex noses, aerials, and assembled devices.

Emphasising here the vastness of the industrial effort, the avalanche of stuff, materials, parts, people, orders, charts, specifications, drawings, and performance data that was being unleashed, has a simple reason. It will allow us to better understand the kind of

[679] See Dee diary excerpts, esp. entries 15 May 1940; 5 June 1940; 8 August 1940 in scrap book, p.85, BL 1.1; Personnel chart 'Group 12', c. 1941, BL 1.2; also see, R.C. Alexander (1999): chapter 8, 9.

[680] Memoranda 22 March 1937; 31 March 1937, AIR 2/1885; a good impression of the wide range of projects underway is given by 'Progress in Research and development', Report no.1, October 1943, AVIA 7/2253. For an accessible, but history of the British radar effort, see Zimmerman (2001); also see Edgerton (2006b): chapter 3.

[681] See reports on operational use, 1943, AVIA 7/2064

[682] Hodgkin to his mother, 1 August 1943, HDGKN A.149

transubstantiation at stake. The point will be to imagine this world as infused with numbers, or rather number-things – numbers as embodied, material entities rather than in terms of discourses of (disembodied) 'information'. Numbers as data on papers, data processed, things measured and tested, numbers used and computations performed. And not least, it will allow us to better to understand the type of scientist that Hodgkin, as part of this world, became in the process: Someone tuned to this numerical ontology in very practical and mundane ways. Second nature.

A first glimpse of what is meant here by this mundane ontology is afforded by Hodgkin's first contacts with radar. '[W]hat I am doing is very long range', he wrote home still in 1940.[683] Working, initially, with Lovell and Robert Hanbury Brown, an Air Ministry electrical engineer, the problem Hodgkin had been set concerned the radar aerials suited for airborne use, and thus, the subject of 'wave guides'. As his notebooks record, upon his arrival at TRE, Hodgkin deeply immersed himself into the matter and calculations of 'radiation patterns' in particular.[684]

For Hodgkin, though well-versed in electrical formalities, this was challenging subject matter. A wave guide, or 'electromagnetic horn', crudely, was a cylindrical metal element capable of generating particular wave patterns. Maxwell's equations and other difficult things (such as the theory of dielectrics) were central to penetrating these patterns whose real-life complexity violated the ideal situation of physical analysis. But this formal impression is quite misleading. By 1940, Hodgkin was wrestling with a technical, engineering problem: 'physically realizable' waves.

Towards the late 1930s, 'possible commercial applications' in electrical communications had spurred considerable interest in these tubes, and they held much promise now as a source of radar scanning beams.[685] Hodgkin was busily excerpting the

[683] Hodgkin to his mother, undated (1940), HDGKN A.144
[684] See esp. 'Radar Notebook', St Athans 1940, HDGKN C.68
[685] Chu and Barrow (1938): p.1521.

pertinent literature, especially, the work of MIT electrical engineer W.L. Barrow. This would have been most easy to secure courtesy of an increasingly elaborate TRE library service circulating and abstracting everything from the *Bell System Technical Journal* to the *Model engineer* to the *Wireless Trader* (in late 1941 it even was decided 'to train one of the [library] girls in the art of photo-copying' to deal with articles in heavy demand).[686] And Hodgkin, we may imagine, must have had some painful memories of the tubular squid axon when contemplating now the mathematical analysis of an 'ideal' 'hollow-pipe transmission line':

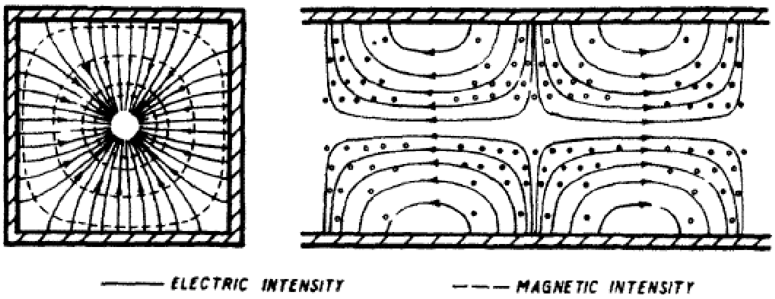
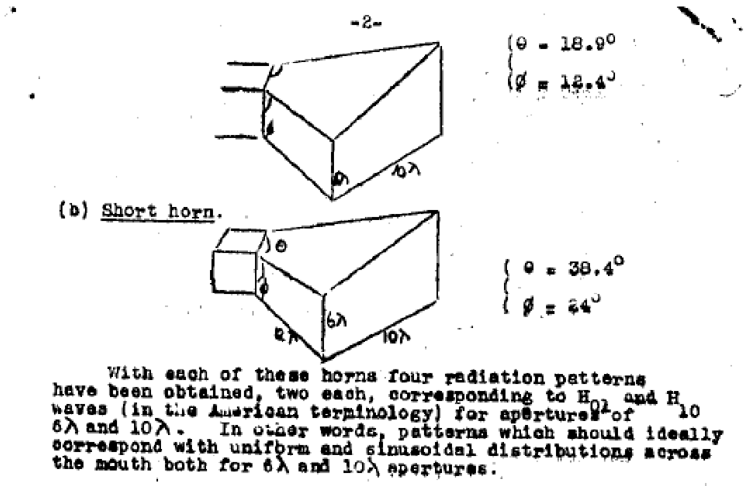


Fig. 2—$E_{1,1}$ wave.

Figure 43: A 'physically realizable' wave in a hollow tube, 1938

Barrow's 'Theory of the Electromagnetic Horn' was not mere theory. It was a theoretical device geared towards the 'design of horns', as he wrote, 'in a thoroughly engineering manner'.[687] Hodgkin indeed spent most of the spring 1940 sitting in a trailer fitted up with measurement equipment and designing, as it were, particular radiation patterns. Different experimental horns (fed with a special valve) were tested, proto-type scale models developed, their radiation patterns measured and plotted as so-called polar diagrams.

[686] See minutes of the TRE 'Library Committee', in BL 7/2
[687] Barrow and Chu (1939): p.64.



-2-

(θ = 18.9°
(ϕ = 18.4°

(b) Short horn.

(θ = 38.4°
(ϕ = 44°

With each of these horns four radiation patterns have been obtained, two each, corresponding to H_{01} and H_{10} waves (in the American terminology) for apertures of 6λ and 10λ. In other words, patterns which should ideally correspond with uniform and sinusoidal distributions across the mouth both for 6λ and 10λ apertures.

Figure 44: Horns tested by Lovell and Hodgkin, 1940

'The principle of models may be made full use of in the design of horn radiators', Barrow wrote in 1939. That principle, made ample use of now by Hodgkin, and heavily supplemented with work on 'optical analogues' as aids to the imagination, was one of scale models and dimensional principles. It formed piece of an engineering approach where mathematical models didn't enter so much as explanations than as tools, in Barrow's words, to 'accomplish specific results'.[688] These models were aids to designing material devices capable of generating particular physical effects; in this case, specific wave 'types' with particular shape, aperture and beam width.

Although we ultimately will make some sense of the notion that the real, physical nerve impulse Hodgkin and Huxley will go on modeling too was *designed*, the suggestion here is not that the exact-same formalities or techniques resurfaced in the biophysics of nerve. What this vignette does very well, however, is to point us to what will concern us much more: the proliferation during the war of routines of modeling practice and as a concomitant process, their banalization - for many more. The emphasis here is on proliferation, accordingly, and as the next section is going to argue, this process was surrounded by the proliferation of a range of similar techniques and devices that generated

[688] Barrow and Lewis (1939): pp.49-50 and see 'Preliminary Report on the Production of Narrow Beams', 13 August 1940, TRE REF 4/4/217, copy in BL 4, file 3.

or served to manage, effectively, with numbers and quantities. They all formed part of the second nature that was being cultivated here: 'production outlook' as one radar-teacher called it.[689]

The increased production-orientation, meanwhile, was strongly felt at places such as TRE, and by scientists in particular. In early 1944, Hodgkin's good friend Lovell informed Rowe of this 'basic reason why we feel that our great days are over': 'the original sources', he opined, 'which made such things as cms. possible ha[d] dried up.'[690] It was certainly true that centimetre radar - 'cms.' - belonged to the more academic end in Britain's radar effort.[691] But someone like Hodgkin, as we have seen, would be ill-imagined as simply a researcher. He was a node in the material flows of this large-scale development and production effort: As the days and weeks slipped by, Hodgkin gradually transformed from an academic bench scientist into a more hybrid persona, a designer, organiser, inventor, equipment tester, and eventually, team leader busy negotiating and communicating with industrial firms, engineers, mechanics and 'users'. From 1941, Hodgkin thus frequently found himself dispatched to the nearby aerodromes, busy with fitting prototypes on planes and test flights with EMI engineers, or indulging in 'almost continuous travelling' for days without end:[692] Promoted to Senior Scientific Officer, Hodgkin found himself in charge of a small team overseeing the development of the scanning and display components.[693] His notebooks of those days recorded 'troublesome meetings' with engineers; countless visits to firms based in London and Manchester; entire days spent with the G.E.C. research laboratories at Wembley; 'demonstrations' witnessed of small-scale models made of the 'gadget' – a radar 'scanner' – the development of which he by then had been put in charge of. 'All this is rather exhausting and leaves you with the unsatisfactory feeling of doing

689 'University Radio Syllabus 1942-43', Report April 13 1943, LAB 8/506
690 Lovell to Rowe, 19 May 1944, BL 7/1
691 As quoted in Lovell (1991): p.58.
692 Letters 9 February 1941; 19 March 1941; 18 July 1941, HDGKN A.146; 26 June 1942; 22 August 1942, HDGKN A.147; 4 August 1942, HDGKN A.148; and Hodgkin (1992): pp.164-165.
693 Hodgkin to his mother, 19 January 1943, HDGKN A.149

nothing except talk and travel.' [694] '[M]y own job', he mused, 'becomes daily less like a scientist and more like an organiser'.[695]

Double spaces

'[P]erhaps as a result of the unscientific nature of my ordinary job', Hodgkin's mind returned to biology more often in those days. Hodgkin more eagerly sought out 'gossip in an academic kind', and similarly displaced people as well. One Thomas, for instance, whom he befriended and who used to be a 'Zoology lecturer at Queens and is now a Radiooperator in fighter command'.[696] And early 1944 saw Hodgkin making a 'great effort' to go back to his pre-war work; returning again, that was, in the evenings to the notes, data and calculations he had had to store away in 1939. Huxley, meanwhile working for the Admiralty, also went back to nerve, analyzing old data in his spare-time. 'It's awfully tantalizing', he lamented, 'working on this at odd times'.[697]

Apart from the occasional 'long walk' in the meadows around TRE, Hodgkin's contact with Huxley had been sporadic. Huxley had been recruited into work on 'antiaircraft gunnery', first with the War Office, and from 1942, the Admiralty.[698] Along with Leonard Bayliss (also a Cambridge trained physiologist), Huxley and David Hill had initially worked on problems of 'fully unseen A.A. fire control'.[699] His life then broadly would have resembled Hodgkin's at TRE, or that of his future colleague Keynes at the Army Signals Establishment. There was little time during these days for the problems of biology. But, these problems never fully vanished even during their collective 'black-out'.

True, committing time to them was 'a little tiring' given the circumstances, as

[694] Hodgkin to his mother, 4 August 1942, HDGKN A.148
[695] See letters Hodgkin to his mother, esp. 19 October 1941, HDGKN A.147; 19 January 1943; undated (December 1943), HDGKN A.149
[696] Hodgkin to mother, undated (March 1943), HDGKN A.149
[697] Huxley to Hodgkin, 13 March 1945, HDGKN C.158
[698] Hodgkin, 'Report on A.F. Huxley's qualifications' (1949), HDGKN H.16; Hodgkin to his mother, 31 May 1943, HDGKN A.149
[699] Hodgkin to mother, 31 March 1943, HDGKN A.149

Hodgkin soon learned, and given the nature of the problem. It mostly meant 'exploring' 'all sorts of puzzling results' from a theoretical angle: 'membrane calculations'.[700] This meant working through the possible scenarios - dynamics of ionic concentration changes – that would hopefully *reproduce* the observed 'curves'. 'I'm quite hopeful', as Huxley wrote very late in the war, 'that the result may look quite Cole + Curtis' picture.'[701] Forced *desk* work: evenings spent with paper and pen rather than electrodes and dissection scissors. The double space Hodgkin was then living found material expression in his notes, where, jotted down on pink TRE sketch sheets, membrane calculations and curves made their appearance next to memos and minutes of meetings.[702]

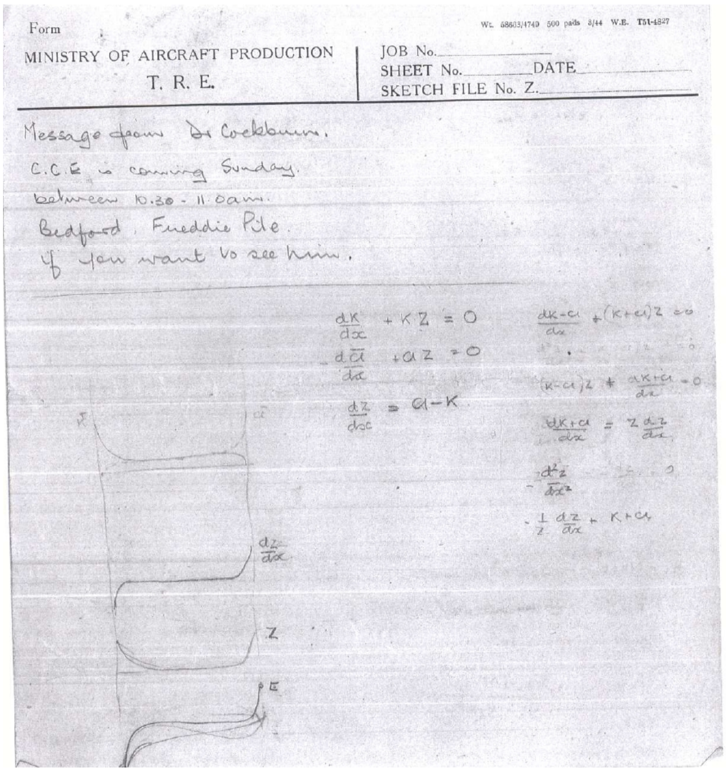


Figure 45: Biological theory at TRE, c. 1944

More will be said about these resumed membrane calculations later, but for now, let us take seriously this image of a *double space*. In those years, it was not empirical advances, or experiment, that transformed the cell. Re-casting of the nerve impulse as a calculable

700 See letters Hodgkin to mother, 9 December 1943, HDGKN A.149; 19 January 1944, HDGKN A.150; and to Rushton, 25 February 1944, HDGKN A.170
701 Huxley to Hodgkin, 13 March 1945, HDGKN C.158
702 'Message from Dr. Cockburn', c.1944, in HDGKN C.159

physico-mathematical entity was about *ways of seeing* a problem, and handling it. One gradually began to see possibilities, paths to proceed, where there previously had appeared insurmountable limits to the imagination (and not least, therefore, practical ones: limits set by computational labour). But to see this, a broad view on developments is required. This shift was not only about one specific problem, technique, or 'principle' (such as the one above). It was as much about a world where numbers quite generally became more palpable, and real, rather than imagined.

When talking about *numbers,* or even, a numerical ontology, it is exactly the normalcy of such intermingling that will figure; far less so, the war-induced advancements of science and technology.

Consider the notes Huxley's boss Blackett aimed at 'new operational researchers' three years after their 'circus' had first taken up its work: Their methods had been 'implicit' but in 'general use', these notes informed, whenever a branch of science had had to deal with 'numerical data about phenomena of great complexity'.[703] Made explicit, these notes illuminate the kind of intermingling, or doubling, and the ways of seeing and handling that mattered: The first step, Blackett advised, when dealing with such a problem of great complexity was to 'collect' as much data as possible, as numerical as possible. The result would be an initial 'numerical picture', 'in the form perhaps of tables or curves' for the 'suitable presentation of the actual facts'. The more demanding step following such numerical proliferation was to find a 'scientific explanation' of these facts: these 'actual facts' and the 'actual tactics' had to be 'related' with the aim of predicting the 'effects' of new weapons or operations.

The way to proceed to cast such a numerical picture into mathematical form – usually differential equations - was through approximation procedures or 'trial and error', as Blackett advised the novice. Blackett casually but very definitely dismissed here what he

[703] Blackett, 'Note on certain aspects of the methodology of operational research' (May 1943), copy in AVHL I 2/2

called the 'a Priori' method or construction from 'first principles'. This, lead nowhere: insoluble equations, less amenable to iterative approximation techniques, and rarely allowing 'practical conclusions' to be drawn. This was obviously 'useless' although 'in times of peace, … this method alone may be possible'.[704]

To be sure, radar *was* highly esoteric content at times, and highly secret too, mentioned 'only in a hushed tone' and 'at rare intervals' - a 'mysterious device', 'which can reach out and "see" through clouds, fog and darkness'. [705] Not least for this reason, as we shall see in much more detail, it brought our actors into intimate contact with the new science of electronics, and a whole new world of electric *micro-dimensions* (more on which in the next chapter). But seeing things from the *high-tech* end obscures these other, more mundane ways by which we can understand (for our purposes) the gradual reformatting of the cell - and its models.

This, after all, was very much a war of numbers. In 1939, the Central Register of the Ministry of Labour had ascertained the availability of 17,954 accountants, managers, administrators, actuaries and statisticians in the event of war - as compared to 4,683 research scientists.[706] Son David, Huxley and his colleagues, as A.V. Hill very approvingly observed in 1940, now spent 'night and day with guns and other apparatus'.[707] There was a war being waged of machines, things, and stuff, not always necessarily mysterious gadgets, but which had to be tested, analyzed, assessed, improved, assembled, counted, shipped, calibrated, installed and adjusted.

Flowing from the midst of things was an unprecedented stream of numbers, and thus paper - charts, listings, diagrams, plottings, calculations. It could mean, as it did for 'operational researchers' David Hill, Bayliss and Huxley, testing the methods of rocket-use

[704] ibid.
[705] nn. (1945): p.47.
[706] Central Register Advisory Committee, Appendix to agenda for meeting on 20 May 1939, T162/1025
[707] Hill to Fowler, 4 October 1940, AVHL I 3/19

in 'unseen fire' by statistical means, plotting, charting, measuring and studying the behaviour of machines and mechanisms or devising 'experimental models' of such gear.[708] Or it could mean, as it often did for Hodgkin, 'nothing except talk and travel.'[709] And it meant, therefore, the 'selling' of ideas and gadgets to superiors and stubborn service people; 'demonstrations', negotiations and fights over specifications, and thus all manner of models and prototypes, diagrams, plans, and charts.

The social life of these newly acute models, diagrams, and charts, was as epistemologically banal as it was practically essential. A 'characteristic' of modern industry, as *Popular Mechanics* then spelt it out for everyone, was 'the complexity of the ingenious devices'. Such 'often taxe[d] the average human capacity for understanding', or so it was reported in 1941, and brought with it 'a new problem', namely 'the difficulty of visualizing and pre-testing these entirely novel and untried scientific and mechanical wonders.'[710]

Modern industry had long turned to the use of models as 'aid[s] to the imagination' 'precise in form, scale and operation.' As the article explained, of recent, 'under the impulse of war', the above problem, and its solution, had gained in scale and importance a 'thousand fold'.'[711] This was the mundane world of numbers and models - newly acute normalcies rather than novelties – in which Hodgkin and his fellow radar scientists had to operate. Learning to 'fit in properly', as it was noted by Cambridge physicist Ratcliffe, to whose tasks belonged the introduction of the new arrivals at TRE, involved such basic skills as knowing how to read circuit diagrams and engineering drawings and being at home with the 'technical jargon'.[712] 'Often the only way of telling somebody else one's ideas on what one had designed', one of Ratcliffe's practical insights into the sociology of science went '[was] to make a proper drawing of it.'

[708] E.g. D.K. Hill, 'The 3" rocket (A.D. fuze) in the role of H.A.A. for unseen fire' (February 1942), in AVHL I 2/3; Bayliss, Army Operational Research Group Memorandum No.615 (1945), copy in AVHL II 4/7; on this unheroic picture of 'operational research', see esp. William Thomas (2007).

[709] Hodgkin to his mother, 4 August 1942, HDGKN A.148

[710] (1941).

[711] Ibid.

[712] 'University Radio Syllabus 1942-43', Report April 13 1943, LAB 8/506

'This [was] the language understood ... in the workshops', he informed a convention of 'radio teachers' in 1943, and 'university men' now better learnt to speak it as well.[713] We may imagine how Ratcliffe or Hodgkin shrugged when some seven years later, when the cybernetic 'fad' was just reaching a peak, someone like J.Z. Young made his appearances on the radio – 'highly stimulating ... [and] quick, vigorous, imaginative' unlike the 'usual scientist', as one BBC official judged - and explained in the 'lingo' of the communication engineer how 'Science consists in exact description of one's observation to other people'.[714]

In chapter 5, we will see how in the post-war period, in a similar proliferation of data, measurements, and quantitative determinations, the substrate of cellular behaviour began to resemble this state of affairs quite definitely. Partly for this reason, the cell's behaviours themselves were more highly resolved - as part of the complex fabric of a newly electronic world. And partly for this reason, the *definite picture* of nervous activity Hodgkin and his fellow returnees would work into this numerical fabric was not only definite, or 'an exact description to other people'. As such, it was an expression of these mundane ways of seeing and handling numerical problems.

It was *second nature*, as Hodgkin's TRE colleague Pringle said in 1946, and who himself promptly jotted down a grand 'programme' for an 'Institute for Synthetic Behaviour' upon his return to Cambridge in 1945. The Institute (never meant to be) would have assembled biologists (to 'supply data and ideas') and engineers – 'Radio and mechanical, including expert modellers'.[715] These were the practices becoming 'socially acceptable' now even in biology, as one U.S. AIR FORCE biometrician discerned in 1950. Models of nerve were one of his notable examples: 'How come we by creative scientific thought?', he asked. 'Models' was the answer: 'the probes by which scientific man can feel

713 Ibid.

714 Notes on J.Z. Young (undated, c.1948) in File 'Prof. J.Z. Young, Talks 1946-1959', BBC Archives, Reading; also see Young to Wiener, 28 November 1951, MC22, Folder 143, Box 10; and see J.Z. Young (1951): esp.p.8; p.42.

715 'The Institute for Synthetic Behaviour' (November 1945), PRINGLE, c.946, Folder b.22

his way' along the path of 'maximum progress'. Less general than theories ('a verbalization of some sort') and not of a 'linguistic style' either, models would enable, not least, 'thorough communication among scientists of different disciplines'.[716]

Formal models, charts, diagrams – 'suitable presentations' -, it is quite true, had become a more definite part of the practical epistemologies of science. But if they did so, as we have seen, it was because they had turned more not less mundane and certainly not, because of the provocative qualities they could indeed assume in the hands (and mouths) of the cyberneticians. For the likes of Hodgkin, models went without saying. But there is more to be said about the numerical ontology that was taking shape still here and now. The remainders of this chapter will be concerned with what remained, for the time being, a more virtual transformation: the re-casting of the action potential problem into a computational one.

The 'sweat of working these things out'

If the war provoked and intensified the sheer mass of models, diagrams and numbers in circulation, it also provoked distinctive ways of using and processing them, routines of *performing* calculations: computational practices geared towards solving equations and managing masses of data more speedily and more efficiently. There were, not least, the many calculation-intensive problems of fire-control, ballistics, and hydrodynamics that spurred the development of computational technologies, machinic and even more so, human; and hence, there were such new, or newly important, institutions as the Scientific Computing Service Ltd., the British Nautical Almanac Office, or the Admiralty Computing Service.[717] More palpably and intuitively perhaps, number-things - the

[716] Rafferty (1950): pp.550-554.
[717] Grier (2005): pp.261-264.

differential equations which scientists had used for ages - here began to live new lives and realities. Blackett, under whose direction Huxley worked away during the war on radar-assisted, automatic fire-control ('gun laying'), still during the war gasped at the 'changing' relationships between theory and experiment so induced - or those which he discerned at the horizon. At stake was no less than the 'myth' of the 'autonomy' of theory, raising mind-boggling questions about the 'relation between calculating machines and the object of investigation'. 'In the limit', Blackett pondered, these labour-saving machines would turn into 'a model of the object'.[718]

Not nearly as dramatic as in Blackett's future vision, cellular behaviour too entered into new relationships with these calculation machines. In very literal sense, *describing* cellular behaviour, as we shall see, came to mean *computing*. In the post-war period, the reality effects of these models, making models *perform,* turned into a definite matter of computational labour. It was a process, however, that had it origins in the double spaces of the radio-war. All there was to work with, after all, were data sets. As far as nerve was concerned, the 'action potential problem' was still essentially the same as in 1939: 'puzzling' results: the potential *reversal, missing agents* and a great many curves.[719]

And indeed, the trajectory through the war of the other name behind the Hodgkin-Huxley model, Huxley, provides a veritable cross-section through these new domains of numerical reality, taking him from operational researcher to developer of automatic control mechanisms to human computer. He would emerge from the war with the reputation of a rather 'good applied mathematician. An authority', as Rockefeller Officer Gregg recorded in his diary, in 1948, 'despite his years, on how to bombard.'[720]

Along with the Blackett's 'circus', Huxley's work had gradually moved into the terrain of mathematical control problems - automated radar tracking, or 'aided laying'.[721]

[718] 'Some notes on the relationship between the sciences', ca. 1944, PB/4/7/1/9
[719] Esp. letters Hodgkin to mother, 9 December 1943, HDGKN A.149; 19 January 1944, HDGKN A.150
[720] Excerpt from Gregg Diary, entry 5 March 1948, RF/RG.1.2, 401 A, Box 13, Folder 114
[721] Bayliss, Army Operational Research Group Memorandum No.615 (1945), copy in AVHL II 4/7

And from 1942, now employed by the Admiralty, Huxley had been busy with the extremely time-consuming computation of a projectile's trajectory and corrections thereof. This complex ballistic problem was dependent on a great many empirical variables: gun elevation, muzzle velocity, wind velocity, and more. And it meant, not least, heavy, time-consuming labour. At the time, a single trajectory would consume the equivalent of some two days' work on a desk calculator, while an average firing table would have consisted of several hundred trajectories.[722]

We can see now where we are heading. When Hodgkin and Huxley began diverting time for nerve again, grappling with the numerical *reproduction* of their own and Cole's old experimental curves, Huxley was diverting time from the Admiralty - and thus, from the 'recomputing' of gunnery tables.[723] Gradually, as Hodgkin and Huxley resumed their work on nerve, in spare hours, at nights, on weekends, the real scale of the overshoot puzzle was beginning to reveal itself. Brooding over data and 'traces', it very possibly involved, as Huxley diagnosed in early 1945, quite intricate 'partial differential equations'.[724]

The equations Huxley and Hodgkin considered at the time were of a deceptively simple appearance, equations such as

$$I = -C\frac{\partial E}{\partial x} - \frac{\partial C}{\partial x}.$$

This particular one related the membrane current to the potential (*E*) and membrane capacity (*C*). The latter 'rough' relation would have been of interest, notably, in terms of what appeared in the records as a presumably *non-linear* dependency on the membrane potential of the ionic current flow through the membrane (collapsed in *I*).[725] There was no simple correlation, that was, between the potential on the one hand, and the ionic concentration differences on the other. Something else, some additional agency or process,

[722] Dederick (1940); Polachek (1997).
[723] A.K. Solomon (1993): pp. 100-101.
[724] Huxley to Hodgkin, 19 March 1945, HDGKN C.158
[725] See loose sheets (ca. 1944-1945) in HDGKN, C.159

was hidden in these curves.

But even seeing this, in these terms, was a prohibitively difficult problem – and the required calculations 'very laborious'. 'I imagine', Huxley began to muse, that 'it can be tackled by numerical methods'.[726] Being able to imagine this was not, of course, mere coincidence. Huxley's imagination had not quite remained the same: Huxley, accordingly, was soon toying around with various 'methods' of calculation, and by 1945, he had resolved the only way to proceed was 'borrowing a calculation machine from the Admiralty'. Within months, complemented by books on numerical methods and ready-made function-tabulations which he procured as well, Huxley's materially enhanced imagination made the first inroads into the prior opacity of these equations: 'it makes an enormous difference to the sweat of working these things out', he reported in March 1945. 'In fact, it's quite a pleasant occupation.' [727]

As the war was drawing to an end, he had already 'tabulated a fair range of solutions', busy producing more: *More* solutions for *more* and 'other [ionic concentration] values'. There opened up, because it was more easily produced, not simply *one* numerical picture but a *series* thereof. The 'series of voltage-current curves' he was reproducing, each one of them patiently calculated and minutely inscribed on graph paper, may have departed not too far from producing a series of shell trajectories.[728] It made more real, at any rate, the painstakingly detailed picture of their equations' implications that began to take shape under their eyes.

[726] Huxley to Hodgkin, 13 March 1945, HDGKN C.159
[727] Huxley to Hodgkin, 19 March 1945, 30 March 1945, in HDGKN C.159
[728] Huxley to Hodgkin, 19 March 1945, 30 March 1945, HDGKN C.159

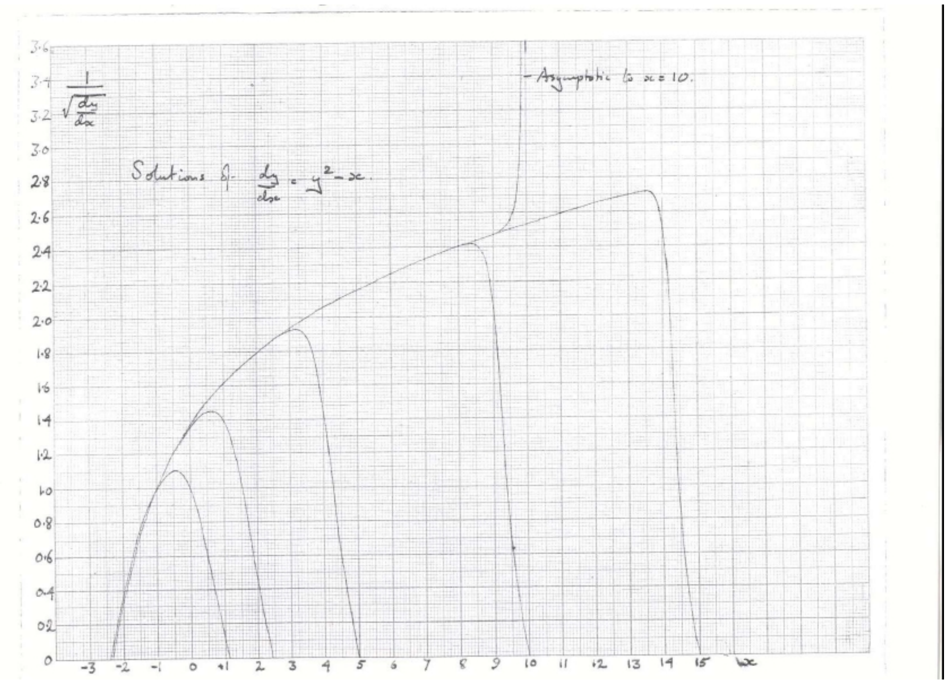


Figure 46: Curve produced by Huxley, ca. March 1945

This was the cell's abstract material one had to work with. No, or little, additional data had accumulated since 1939.[729] Progress in this connection was 'practically nil', as Cole said.[730] What had profoundly begun to change, however, in the six years since 1939, was the space where the problem could find a solution. What had changed profoundly was second nature: the one of Hodgkin and other diverted men, and the one of abstract things. The type of equations Hodgkin and Huxley now considered in earnest, it turned out, had as solutions functions of functions: they were, in short, problematically intractable, imaginable only with the substantial aid of machines, graphs, charts, and eventually, models.[731]

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Within this incision, there had had been a definite shift underway in the formal perception of cellular behaviour. There led, to be sure, no direct line from here, or for that matter

[729] See e.g. Grundfest (1947).
[730] Cole to Hodgkin, 1 February 1945, HDGKN H.1
[731] Huxley to Hodgkin, 19 March 1945, HDGKN C.159

gunnery tables and hollow tubes, to the model of the axon. The path the impulse problem, however, was then taking a similar trajectory. It had become a computational problem, amenable to computational techniques. This was the new *shape* the problem assumed.

There was not nearly a solution in the making, let alone, a model. What these new numerical realities *did* reveal was primarily something negative: the absence of sufficient and sufficiently detailed empirical data, and in particular, according to Huxley, a 'more extended knowledge of membrane conditions' - computational progress notwithstanding.[732] None of these calculation-efforts made their way into the comeback paper Hodgkin and Huxley had submitted to the *Journal of Physiology* still in February 1945. This, as they wrote, merely was to provide a more detailed account of the results they had obtained in 1939:

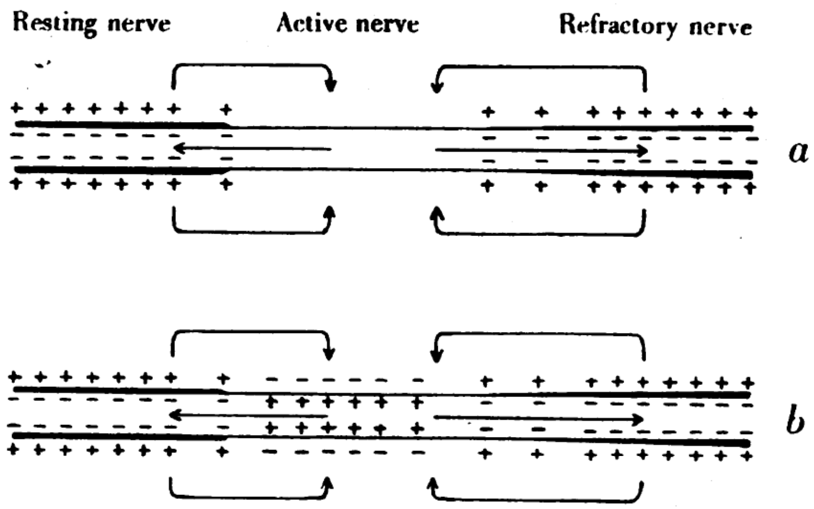

Figure 47: No 'classical picture', 1945

The 'classical picture' ('a') of a simple membrane breakdown, the message went, had to be 'altered'. Something else would have to account for the reversal of the potential, here depicted in 'b'. Their paper contained no public trace yet of a *quantitative,* theoretical reconstruction of this non-classical state of affairs.[733]

[732] Rushton to Hodgkin, 29 March 1945, HDGKN H.2
[733] Hodgkin and A.F. Huxley (1945).

Conclusions

In between 1939 and 1945, the situation regarding quantitative descriptions of the cell, what was perceivable and conceivable as possible, had made substantial leaps. When Kenneth Cole resumed contact with Hodgkin in early 1945, himself having endured a 'four-year blackout', to inform him that 'problems which are involved in nerve' would 'require a differential analyzer or something equivalent', Hodgkin and Huxley, as we have seen, had long arrived at the same conclusion.[734] Cole and Curtis indeed had been going down that route as well, and they too had been distracted from 'nerve' - by problems of radiobiology.[735] Even Cole's maths now failed him, or so it must have seemed to the trained engineer when in 1942, shortly before joining MetLab, the Chicago branch of the Manhattan project, he had approached the Institute for Advanced Studies, Princeton, in the hope of 'obtain[ing] help with [his] rather formidable mathematical problems'.[736]

These rather formidable problems Cole had discerned in the same puzzling results which troubled Hodgkin and Huxley: the overshoot. They too were those of non-linear processes, a mathematical subject then still in its infancy. For their part, the 'reversal' had convinced the two American biophysicists that the membrane could impossibly be conceived any longer as a simple 'linear' electrical element. Instead, the reversal - or what they framed as a 'non-linearity' - they suspected to reside in an 'inductive membrane element'. A 'complete [circuit] representation' of the membrane, they had argued in 1942, would have to be based, somehow, on such an element.[737]

Similar non-linear phenomena, it turned out, were in fact exhibited by various 'inanimate systems' as well. These now populated their no-longer linear, electronic life-

[734] Cole to Hodgkin, 1 February 1945, HDGKN H.1
[735] Note 'Re: Kenneth Cole', 25 March 1942, RF/RG 1.1 Box 133, Folder 1651; and Miles (1972).
[736] Cole to Rappleye, 9 October 1940, COLE/Columbia
[737] Cole (1941): p.42; Curtis and Cole (1942): pp.142-143.

worlds: the ‘recently developed Western Electric 1-A Thermistor’, for instance, and ‘technical rectifiers’ and piezoelectric crystals to which Cole then promptly was pointed by engineers of the Bell telephone company.[738] Indeed, a whole range of ‘physical structures’ exhibited ‘analogous’ non-linear phenomena once one learnt to see them. In the post-war period, these phenomena soon were found to be present in systems ranging from frog stomach mucosa to ‘artificial model membranes’ such as porous glass discs, cellophane and charged collodion membranes.[739]

These ‘time-varying’, ‘non-linear’ responses of biological membranes turned into a major puzzle for membrane biophysicists during the early post-war years, and they framed much of the debates revolving around the putative ‘ionic picture’ underlying these transient events. It was exactly these non-linear processes which frustrated a certain Norbert Wiener in his ‘experimental programme’ on a ‘rigorous description of the time-course of the spike potential’. The immense frustrations Wiener experienced with these simple and prosaic nerve axons - an apparently ‘excellent place to try out mathematical and experimental methods’ - may seem ironic, but here they do underscore the newly abstract nature of cellular behaviour that has been the subject of this chapter: quite unexpectedly, Wiener’s work suddenly revolved around trying, by mathematical means, to ‘quasi-linearize that very non-linear system’.[740]

Wiener, in fact, failed to advance the subject much along these lines, and so did Cole, despite the latter’s privileged (or illicit) access at the time to classified mathematical treatises on non-linear mathematics.[741] In the post-war period, to make this system describable - amenable to being modelled - indeed required its *linearisation*. But significantly, this happened very literally so, materially: the axon itself, as we shall see in the next chapter,

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738 Debye to Hanson, 30 September 1941, RF/RG 1.1 200D Box 133, Folder 1650

739 Teorell (1949a): esp. p.213; pp.218-219.

740 Wiener to Rosenblueth, 23 September 1946, MC22, Box 5, Folder 71; Wiener to Grey Walter, 21 November 1951, MC22, Box 10, Folder 143; Wiener to Fremont-Smith, 25 April 1946, MC22, Box 5, Folder 70

741 Miles (1972).

had to turn part of an electronic circuit first.

Pursuing this other dimension of the cell's abstract ontology will require us to continue interrogating the mundane, material world of the radio-war (and its aftermath). Here, the focus has been on the seemingly more abstract entities which came to figure prominently in the war-effort: modeling-strategies, computational practices, but also, a whole range of related, and equally mundane technologies like charts, diagrams, and plots. Together they added up to the second nature the men like Hodgkin acquired during those years. Together they created newly palpable realities for abstract things - realities which began to engulf the behaviour of the biological cell.

These were matters of scale, and material rather than discursive transitions and intensifications. What this chapter has suggested more broadly is to take these banal practices and items on board as we think about historical change in this connection - and thus about the new, and newly dominant epistemic roles for models in science.[742]

[742] On this, see esp. Cohen-Cole (2005); also see Crowther-Heyck (2005); Shapin (2008).

TOYS for MEN ONLY

Preparing scale-model plane, above, for wind-tunnel tests at California Institute of Technology. Below, scale model of Mount Palomar observatory dome used to check wind, rain and snow loads

WORK is mere play for the research engineers. At least, that's how any small boy would look at it if he saw these grown men tinkering with toy trains and planes, boats and automobiles, electric motors and compression engines.

But if you could examine all the playthings of all these engineers, you would enjoy a glimpse into the world of the future, for the toys of today are working models of the mechanical marvels of tomorrow—reflections of engineering visions.

Toys have had a profound effect on human progress. The gyroscope, for example, was merely a toy until its properties were applied. Then it grew up to fly airplanes and steer ocean liners. Boys sent electric trains dashing around toy tracks long before railroads used electric locomotives, and operated toy machines with miniature electric motors while the wheels of industry still were being turned by steam.

Today trains cling to the rails better, automobiles run more smoothly and planes travel faster partly because research men have learned valuable lessons from toys. Without working models, engineering and scientific progress in many fields would be retarded greatly because man still would be forced to learn by the costly process of trial and error.

When the modern engineer starts to design a new airplane, a new car or a new boat, he first evolves a plan which appears sound in theory, something which "looks all right on

Walking wooden doll, top, which displays same sort of vibration that causes machines to shake apart. Bottom, scale-model locomotive boiler in which corrosion-resisting agents are studied

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Figure 48: 'Work is mere play for research engineers', October 1938

What the embryologist/operational researcher Waddington in his *The Scientific Attitude* (1941/1948) proposed to 'call "the model method"' was casually extolled by many in the post-war period.[743] The function was 'plain', as Cambridge applied psychologist Kenneth Craik said in his widely influential *The Nature of Explanation* (1943) when he discussed how 'the organism carries a 'small-scale model' of external reality … within its head'.[744]

If the function was 'plain', this chapter has suggested some answers as to why. The argument was not that such plainness was uniquely precipitated by the war as examined here. The latter merely concentrated ways of doing and thinking that have long been prepared in other sites and places, but that we tend to attribute too casually to less banal figures and scenes, notably cybernetics. We know, unfortunately, very little about these cultures of *banal modeling* I am advancing here. There *is* every reason to suspect they were

743 Waddington (1948): p.126.
744 Craik (1943): pp.60-61.

vast, even before the war. We know bits - about interwar wind tunnels for instance, and scale models in aeronautical engineering; about analogue electrical scale models of power and telephone networks; or, on the far end of the spectrum, but no less pertinent, a few things about constructions of boyhood, model-building and engineering virtues.[745] There was no epistemic revolution ushered by this war, and no homogeneous discourse. In 1957 young, female BBC listeners still 'found the word 'model' very confusing', at least in its new epistemic nobility, 'as to the non-scientist this conjures up the picture of a mechanical model and not a 'conjecture''. To those many young men who returned from a scientific war, however, Hodgkin and Huxley included, it was common staples, hardly worth mentioning.[746]

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745 Hashimoto (2000); Sterrett (2006); on network models, see Mindell (2002); on boys/engineers, see Alcorn (2009).

746 'Talks for Sixth Form. 'Man and Machine'' (listener feedback analysis, 1957), in File MacKay, Talks I: 1949-1962, BBC

(5) ELECTRONICS.

Re-engineering the Impulse:

Electronics, trace(r)s and the post-war biophysics of nerve.

> *Alan Hodgkin, F.R.S., Cambridge.*
> *Unwilling to broadcast during the next twelve months.*
> *(memo by Archibald Clow, 28 May 1952, 'Third Programme Science Talks')* [747]

Squid season. 'July 2nd [1947] … 12" Mantle-length Squid. Squid Mounted. Dissection started 4:30. A[ction] P[otential] OK in trunk and after cleaning 7.20 pm. Axon dia[meter] … 632 μ … but variable…' 8.52 pm: baseline 0, medium saltwater, action potential 30.7 mV. 8.56 pm: action potential 31.7 mV, baseline 15.4 r, 6.5 l, short circuited. 8.59 pm: Camera on, stopwatch on.[748] When the fishermen brought in the squid – hopefully in good condition – the animals were hurried into the labs, and their axons quickly dissected out and kept 'alive', at least for several hours, in sea-water; next, a microelectrode is carefully inserted into the fragile axon, electrical constants and diameter of the axon measured; the volume of the fluid outside the axon determined. It follows: electrical measurement of external volume, test solutions, the redetermination of constants, the final calibration of the arrangement - of amplifier, input stages, recording system, micrometer stimulation electrode. The 'experimental test' could proceed.

Sometimes fifteen, sometimes twenty axons might have been available on a good day, and not every axon in fact was 'good' : 'trouble with first two axons. Not coming out

747 R51/523/7 Science, 1947-1954, BBC Archives

748 Entry 2nd July, 'Tidy Notebook' (1947) in HDGKN C.19

clearly etc.', an entry in Hodgkin's 'tidy' notebook from 1946 read. 'Several obviously in bad condition. Axon 1 low resistance type. Repeats with difficulty.'[749] Axons became useless once 'virtually dead', constants 'difficult' to determine (as axons easily failed to 'recover'), amplifiers 'drifted'. Columns and columns of data began to fill up 'rough' and 'tidy' notebooks.

Hodgkin and Huxley had returned, 'very much enjoying to be back'.[750] One experimented again, measured, and calculated; without too much talking. Hodgkin and Huxley had turned into electro-engineers not just appropriated their 'lingo', or the utopian dreams of a fully automatic, electronic world of communication, in the hope of finding 'common ground' among workers of different branches of science,[751] or in certain cases, as their friend J.Z. Young explained it to Norbert Wiener (as if the latter didn't know), so as to reach a 'very wide audience' with these new horizons.[752]

The world of cellular behaviour indeed was changing. Walking into the laboratory of the Cambridge 'nerve team' one perhaps might have hardly noticed the difference. Electronic gadgets were replaced by the latest models, but one encountered, basically the same experimental system one had left in 1939: squid giant axons, amplifiers, a micro-electrode. A season-dependent article, the cycle of the squid, now as before, shaped the scientific life in question: Experimentation during summers and autumns, interpretation and analysis concentrated during the winters. Empiricists half the year, interpreters and theoreticians for the remaining months. The phases of data-processing truly began as biophysicists packed up their equipment and moved back from the sea shores to the academic inland. Here one was closer to the books and literature; here, there was time for *desk-work*; Brunsviga calculations machines stood ready: a seasonal arrangement not

[749] See entries May, 'Tidy Notebook' (1946) in HDGKN C.16
[750] Hill to Gasser, 1 March 1946, AVHL II 5/36
[751] Megaw to Bates, 3 September 1949, BATES, A.89
[752] Young to Wiener, 28 November 1951, MC22, Box 10, Folder 143; in a similar strategic vein, see McCulloch to Keener, 5 May 1949, McCulloch papers; J.Z. Young (1951): p.8; also see Bowker (1993).

altogether unlike operational research. As Blackett's advice to the novice operational researcher went: step one: 'collect' as much data as possible, as numerical as possible; step two: compose a 'numerical picture', 'in the form perhaps of tables or curves'; step three: find equations of that relate the 'actual facts' to the 'operations'.[753]

No drastic transformations, to be sure, but the superficial glance might prove misleading. These returnees were not quite the same as before; their minds re-framed in the 'production outlook'; their fingers better versed at the electronic arts; their eyes more adapted to the flickering signals that appeared on the surfaces of oscilloscopes screens; their 'operations' planned. Thus 'the secret of [their] circuitry', and here one 'learnt for the first time how serious planning of scientific work ought to be done', as one visiting post-doc from Switzerland recorded, the first of a long queue flocking to Cambridge.[754] This should be, as one Rockefeller officer declared in 1949, 'the only place in the world to send a young man interested in studying neurophysiology.'[755]

This chapter is concerned with the post-war world in the making here, in all its quietudes. Materially, it was neither radically different from what went before - not teeming with electronic, futuristic technology, electronic brains, or cyborg creatures - nor was it their old, pre-war world these biologists now re-assimilated to. They operated in a post-war world, this chapter argues, that was indeed replete with electronic things, 'electronic assistants', calculation machines, and a host of other 'advances', as A.V. Hill had hopefully diagnosed already in 1944. The new radioactive isotope techniques and the 'great developments in radio' in particular, he submitted, could 'scarcely fail to have biological applications'.[756]

753 Blackett, 'A Note on certain aspects of the methodology of operational research' (1943), copy in AVHL I 2/2

754 E.g. Buller to Hodgkin, 2 June 1949, HDGKN H.15; Lowenstein to Hodgkin, 26 September 1947, HDGKN H.8; Staempfli to Hodgkin, 1 February 1948, HDGKN H.9

755 See Morison to Gregg, 4 March 1949; Morison, interviews with Feldberg, Hodgkin (July 1949), RF/RG.1.2, 401 A, Box 13, Folder 114

756 'The need for an Institute in Biophysics' (December 1944), copy in HD/6/8/6/5/184

This much may sound familiar, indeed expected in light the many historical studies on post-war biophysics. Where this chapter diverges from the literature is the image painted there of departure: a world of novel, expensive instrumentation (think of the electron-microscope), newly established academic institutions, and upheavals in the disciplinary order.[757] Here, the picture will be one of intensification, not incision. Together, this chapter argues, these advances did generate a new kind of model of the cell but it was deeply knitted into a surprisingly inconspicuous world of electronics, numerical practices and, as we shall see, 'ionic events', traced and made present by the new, post-war abundance of radio-active isotopes. The reality effects of this model-cell were material rather than discursive.

The argument, to remind ourselves, was this: that we can understand this pervasive electronic mediation of the cell's newly numerical, electronically resolved substrate in correspondingly *mundane* ways. The depths of these mundane entanglements, I shall argue, made the *decomposition* of cellular activity into its ionic micro-dimensions a very real-life affair indeed. In the post-war period emerged the real-world substrate of what had remained, for the time being, the still largely virtual, but formidable computational problem of cellular behaviour.

The following thus revisits the radio-war in more general terms: as an agent making electronics a common factor in the lives, not least, of a great many biologists. This chapter examines, too, how these confined spaces of war-time electronic technology were re-produced in the post-war world. And of course, it is concerned with what emerged in and between these spaces, replete now with electronics, tracer elements, and other such new 'insignia' of the physiologist:[758] the new realities of cellular behaviour. Almost *naturally*, as we shall see, the model Hodgkin, Huxley and Katz masterly crafted from the world's

757 Esp. Rasmussen (1997a); Rasmussen (1997b); Chadarevian (2002); Creager (2002a); Gaudillière (2002); Kraft (2006).

758 Lovatt Evans (1947): p.91.

electronic substrate would be one of ionic events, electrical currents, and computations. Indeed, in this world, the impulse itself would re-emerge as a different thing: re-engineered.

Post-war visions

'Productivity' in matters of electrophysiology 'had not yet returned to the prewar level' biophysicist Harry Grundfest diagnosed in 1947. But Grundfest, having only recently returned from the Fort Monmouth Signal Laboratories, New Jersey, found few reasons to complain about a lack of new directions.[759] The post-war world was already producing, a whole range of visions of bioelectrical behaviour included. An interdisciplinary *Conference on Bioelectric Potentials* in 1946 signalled the new beginnings - geared towards 'opportunity for free intimate discussion';[760] also in 1946, also in New York City, one on *The Physico-Chemical Mechanism of Nerve Activity*; in 1949, an international symposium in Paris on the *Electrophysiologie des Transmissions et Facteurs Ioniques*;[761] from 1950 to 1954, the Macy Foundation sponsored a series of meetings on *The Nerve Impulse* - as one of the many *besides* the famed one on Cybernetics: *The Nerve Impulse, Panic and Morale, Connective Tissues, The Central Nervous System and Behavior* and many more; in 1952, a Cold Spring Harbor Symposium on Quantitative Biology attracted an even greater diversity of workers. Its topic was *The Neuron.*[762]

In the past, 'opportunities for such informal gathering ha[d] largely been left to chance', as one 'Nerve Impulser', Macy Foundation officer and neuro-psychiatrist Frank Fremont-Smith would reminisce, himself already on the best way to turn the 'informal', interdisciplinary conference into a 'technique' and 'special means of communication'.[763]

759 Grundfest (1947): p.477.
760 Macinnes (1949).
761 See Monnier to Hodgkin, 27 April 1948, H.10
762 nn. (1952a).
763 Fremont-Smith, 'History and Development of the Conference Program', Typescript (ca . 1971, non paginated), FREMONT-SMITH; Merritt to Dear Fellow Nerve Impulser[s], (ca. 1954), copy in MC154, Box 11, Folder 13; on the ideology driving this 'Cold War Salon' culture, see Cohen-Cole (2009).

And there was no shortage of novel, fundamental visions either. Based on a mix of quick-freezing and electro-chemical – so-called polarographic – methods, Alexander von Muralt's *Die Signalübermittlung im Nerven,* issuing from neutral Switzerland, had promised a new, grand 'synthesis' still in 1945.[764] The magisterial *Study of Nerve Physiology*, by histologist-turned-electrophysiologist Lorente de Nó, 'core' member of the Macy Cybernetics group, hit the shelves in 1947, passionately reviving *chemical, electrogenic forces*: impulses were the *products* of 'self-contained … biological machines' not mere side-effects of passive, physical diffusion, the message of these 'Telephone Books' (in virtue of their size (1,000 pages), colour, and readability) went.[765] Meanwhile, M.I.T.'s Francis Schmitt, brought up between the wars on the physiology of nerve and muscle, and now eagerly embracing the electron-microscope, promptly moved on from his OSRD-project on the molecular structure of rubber and collagen ('artificial skin') to the 'structural basis of impulse propagation'. The 'current importance of molecular morphology', he lost no opportunity to emphasize in those heady days of biophysical advancement, was 'well illustrated in nerve problems'.[766]

Not everyone concerned with nerve saw the pattern Hodgkin, Huxley and Katz had begun to see, *naturally*: ionic events, mathematical problems, and electrical currents. The 'kind of electrical double-talk concerning nerve' – circuits, batteries, wires, resistances, capacities - might very well result from certain 'implicit assumptions' as Grundfest would muse in one of these more 'informal' hours, in 1950: assumptions embodied in the very 'gadgets' one employed.[767]

In what follows, this kind of electrical double-talk (and a double-vision, too), and why it was that it was indeed quasi-*natural* for a majority among nerve scientists, is at the heart of the matter. We shall be little concerned with the controversies, alternative visions,

[764] Muralt (1945).
[765] Lorente de Nó (1947): esp. pp.103-105; Woolsey (2000): p.9.
[766] Schmitt, 'Talk to Worcester foundation, 4/29/48', MC154, Box 11, Folder 2; and see Rasmussen (1997a): esp. pp.38-40.
[767] Grundfest in Nachmansohn and Merritt (eds.) (1950): pp.18-19.

or dissenters. As to the character of developments, they were not very defining. '[W]ild-goose chases', as A.V. Hill casually dismissed them; 'speculative' said Hodgkin; 'obscure', Katz. 'Some, more or less in despair', as one Swedish biophysicist aired his consternation in 1949, 'speak in vague and general terms of "metabolism" and "chemical reactions" as sources of these [bioelectrical] potentials'.[768]

Yet when we now reconstruct the genesis of this hegemonic, electro-numeric *model-cell*, let us not forget these other accounts, visions and schemes which formed part of what was, in terms of nerve cells, a busy and far from homogeneous post-war world. But it was dominated by its biophysical micro-dimensions. Highlighting these other accounts here will throw into relief how intimately modeling practice, electronics and cellular behaviour merged in Hodgkin and Huxley's model-cell. Nothing here was vague, and for much the same reason, it was the work of Hodgkin and Huxley, not the Muralts or Lorente de Nós, which unquestionably embodied the epistemic ideals - and popular psychology - of post-war science.[769] Hodgkin and Huxley, as Young's *Doubt and Certainty in Science* broadcast-lectures (1950) had it, showed just 'how far the physiologist can go in talking about the action of a part of the body by comparison with processes that occur outside the body' (namely, a 'battery'). Young smoothly and easily enrolled their *exemplary* science for what appeared to J.B.S. Haldane as a 'new type of metaphysics' indeed. 'No Christian', Norbert Wiener's good friend Haldane commented, 'after reading the first verse of St John's Gospel, can object to the emphasis laid on communication.'[770]

Unlike the dissenting visions of nerve, the electrical gospel, notably as spelt out by Hodgkin, was perceived as 'lucid presentation of difficult matter'.[771] Even Lorente de Nó's *Study,* meanwhile, littered in fact with calculations, circuit diagrams and electrical models,

[768] Hill to Gasser, 1 March 1946, AVHL I 3/22; Hodgkin and Katz (1949): p.37; Katz (1960); Teorell (1949b): p.549; also see Gerard (1947): p.549; also see Feldberg (1954): p.549; also see del Castillo and Katz (1956): pp.128-135.

[769] On this psychology, see esp. Cohen-Cole (2005).

[770] J.Z. Young (1951): p.42; Haldane (1952): p.104.

[771] Davson to Hodgkin, 7 June 1949, HDGKN H.16

resembled a *natural history* of the impulse much more than a synthetic, definite model thereof: this vision of the impulse's 'production' drowned, incommunicable, in 1,000 pages, masses of data, facts, and factors, and innumerable graphs. And not only in terms of their communication did the things themselves resist their biochemical conversion: 'At present, the absence of rapid [biochemical] methods commensurate with the speed ... of the potential' rendered such heresies vague gestures at best, whatever the truth of their faith: that 'in living cells there is more going on than electric circuits'.[772]

These biochemists of nerve, themselves having received major stimulants in *their* recent, chemical war of nerve (gases), in fact rarely engaged with such esoteric questions as the fundamental nature of the nerve impulse.[773] When they did, however, they saw more convoluted entities and processes. They did not see simple ionic currents, or membranes disappearing 'electrically', but rather chemical interactions, metabolic - *electrogenic* - reactions, and complex ionic aggregates: acetyl-choline for instance, and other such putative 'action-substances' (also suspected to have a 'protective' action vis-à-vis certain toxic nerve agents): aneurin (vitamin B1) , the 'aneurin-like' substance 'A4', or multivalent ammonium ions such as TEA, tetraethyl-ammonium.[774] For them, too, the impulse was decomposing, but according to a different time-frame. Theirs was a qualitative, metabolic time: successive 'fractions', as notably the countless tracings of de Nó seemed to suggest. These fractions made up the malleable impulse, endlessly modulatable by chemical means: Q ('quick'), M and L ('labile').[775]

It was a 'psychological puzzle', as one of these biochemistry-minded physiologists sneered, why electrophysiologists were so blind to 'proteins, enzymes and everything modern physico- and biochemistry knows about them.'[776] The 'electrical mode of thought

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772 Grundfest (1947): p.488; Merritt (1952): pp.109-110.
773 The intersections between chemical warfare and knowledge production in the sciences of nerve haven't received much historical attention; see however Schmaltz (2005); also see Russell (2001).
774 See esp. Muralt (1945); Lorente de Nó (1947); Nachmansohn (1947); and see Schmaltz (2006).
775 Lorente de Nó (1947); Hodgkin (1951): p.318.
776 Merritt (1952): pp.109-110.

[die elektrische Denkweise]' was 'completely one-sided', judged another, von Muralt, venturing how the 'only kind of nerve we actually understand' took the 'form of a model'. For real nerve was 'complex'.[777] But nothing in the complicated kinds of 'schemes' he and other (not too many) dissenters cooked up held much appeal to those finding truth now in *electronics* and *communicability.*

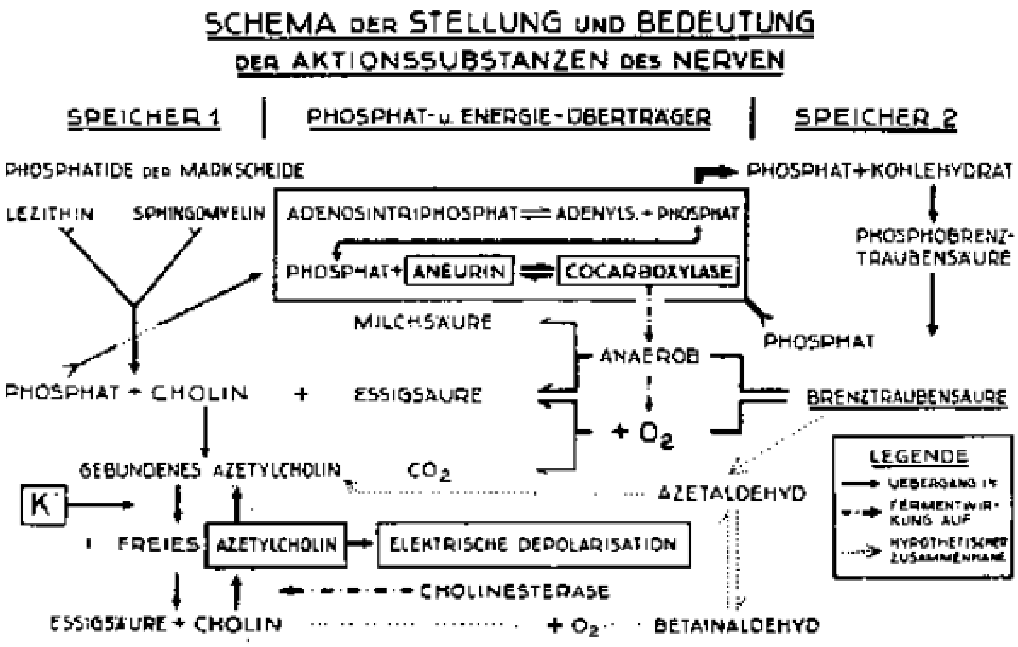

Abb. 124.

Figure 49: 'schema' depicting the putative operation of 'action substances' in nervous activity, 1945

Their numbers, like the numbers and models themselves, had been surging, as we shall see in the following. Like ex-radar biologist Alan Hodgkin, they would return with great developments in mind. During the summer of 1945, barely released from active service, Hodgkin himself already had outlined a 'programme': 'Future Research on Physical Aspects of Excitable Cells'.[778]

Busy pondering the 'experiences encountered during the war years' - or the 'Future Application of Electrical Technique to Biology and Medicine' - Hodgkin soon will be

[777] Muralt (1945): pp.136-138; pp.213-214.
[778] 'Future Research on Physical Aspects...' (ca. September 1945), HDGKN H.1

joined in this project by Huxley, Keynes, Katz, and David Hill: young physiologists now returning to Cambridge, as Adrian gleefully noted, 'with the training and outlook of the physicist'.[779] These reconverted physiologists would form the core of the Cambridge 'nerve team', as Hodgkin's troupe was known - the team that would turn the impulse problem into a model-solution. One would have to 'keep abreast with modern developments in physics', as Katz's own lessons went.[780]

In terms of nervous behaviour, the world they created, and even more so, the world they found, I shall argue, indeed was a bio-*physical* one. Understanding their model, however, means rewriting the accounts we have of this world. It would be wrongly imagined as overflowing with futuristic gadgets, or in terms of a new age of interdisciplinarity, or as one of disembodied information. What made it a *world* were mundane matters of scale: many more diverted people and all manner of electronic stuff. The next section will begin with the former, the diverted people.

Manufacturing personnel

In December 1939, the Scientific Research Committee of the Central Register at the British Ministry of Labour, charged with classifying recruitable scientists came to the conclusion that there was, in this war, 'likely to be little demand for either botanists or zoologists'.[781]

But dawning on them was a tremendous lack of supply in 'telecommunications personnel'. By mid-1940, with the 'radio-war' coming into its own, 'electrical engineering' had officially turned into the supreme scientific 'scarcity category'.[782] For many students,

[779] Carmichael to Hodgkin, undated letter (c. Feburary 1945); and Hodgkin to Carmichael, 18 February 1945, HDGKN A.171 ; 'Application for a Grant for Research into the Biophysics of Nerve...' (October 1945), RF/RG.1.2, 401 A. Box 13, Folder 114

[780] Katz to Hill, 3 June 1944, MDA A6.4; Katz to Hill, 13 November 1945, AVHL II 4/47; Katz, 'Curriculum Vitae' (1945), copy in AVHL II 4/47

[781] Minutes 12 December 1939, Scientific Research Committee, T 162/1025

[782] 'Position Regarding Supply and Demand' (November 1940), LAB 8/873

recent graduates, and even pupils the consequence was to be sucked into the 'wireless' war-effort - irrespective of their actual 'inclinations'. For us, this scientific scarcity category the war generated can illuminate the sense in which the electronic world at stake, and the bioelectrical borderlands it would come to mediate, were indeed this: mundane. Resurrecting the mundane also will remove the air of curiosity surrounding Hodgkin and Huxley's experimental lives. It is hardly appreciated how present the figure of the diverted biologist was in post-war scientific culture; and even less so, how systematically engineered such biographies were: one year into the war, the situation as regards wireless personnel was perceived as 'grave'.[783]

Ever since, the radio-war and its 'beneficial effects' in particular have featured prominently in the historical imagination of British biology.[784] Through the system that was now being installed to mend the situation passed, as radar-veterans fondly remembered, 'scientists of all types, biologists, physicists, mathematicians, chemists and schoolmasters, to be trained in the mysteries of radar.'[785] Of those British biological scientists leaving their biographical traces in the DNB or by becoming F.R.S., for instance, no less than forty were involved with either radar and/or operational research. It is not surprising, then, that these veterans figured largely when in 1975 the Royal Society gathered together its ageing fellows to discuss the 'Effects of World War II on the Development of Knowledge in the Biological Sciences'.[786]

Significantly, these are not the images usually conjured up in connection with the 'physicists' war' - disillusioned nuclear physicists invading and reforming biology.[787] Instead, the biologists voiced reminiscences of attending radar-school, of surplus electronic scrap flooding the universities, or (more familiar-sounding) of being initiated to a different mode

[783] Ibid.
[784] Cited is Pringle and Peters (1975).
[785] Budden (1988): p.687.
[786] Pringle and Peters (1975).
[787] It is a story that carries over even into writing the history of the nervous sciences, see esp. C.U.M. Smith (2005).

of science – team-work, organization, and 'empirical applied science'.[788] These elements will figure quite centrally in the following as well, but the emphasis will be on the scale of the intervention. Scale is important, and not least because the scattered accounts we do have of these diverted biologists tend to conceal more than they reveal of the mundane circumstances of their creation. When, in 1944 already, physicist Bernard Lovell argued that this motley crew's secret of success was the fact that 'the scientific method of approach [was] ingrained in them', he more than anything else gave expression to what David Edgerton argues were to be the dominant, self-congratulatory and narrowly academia-centred accounts of the British scientific war. They 'spontaneously' applied their method, Lovell said, to any 'situation or problem'.[789]

This figure of the diverted biologist – as a a helpful, if unorthodox academic boundary-crosser - spilt over even into the popular domain. The first major celebration of the radio-wizardy that won the war, Ustinov's *School for Secrets* (1946) thus finds Professor Hatterington, a 'specialist in reptiles', summoned to Whitehall, recruited into steering the radio-war research effort – much to his own surprise. He is promptly clued in by a whimsical civil servant: it is certainly not his special expertise Hatterington is wanted for, but his general 'scientific inquisitiveness'. One of the heroes of the radar-novel *Glide Path*, penned in the early 1960s by ex-radar novelist Arthur C. Clark too was a biologist: A true 'King Boffin', in fact, but '[u]nlike most of them, he was not a physicist; he was a biologist with a flair for maths.'[790]

Biologists turned into *boffins*, so much so indeed as to have licensed the floating of self-attributions such as 'ex-radar biologist'. The London neuro-physiologist John Bates, for instance, himself 'ex' Armoured Fighting Vehicles School, Dorset, and an expert on 'manual tracking', had few difficulties when scouting for like-minded 'folk' for a projected

788 Pringle and Rudolph Peters (1975): p.544.
789 Lovell to Rowe, 19 May 1944, BL 7/1; and esp. Edgerton (2006b).
790 A.C. Clarke (1970): p.37.

dinner club in 1949. Known to posterity as the Ratio Club, it was composed, Bates noted, of such specimens as one 'Statistical Neurohistologist', several 'ex radar zoologists at Cambridge', physiologists from 'Adrian's lab' (also in Cambridge), one 'ex Psychologist, Radar etc. T.R.E.'[791]

'Radar etc': the rhetoric of scientific inquisitiveness and flair, however, is a misleading one. So is, on the whole, the idea of an 'ingrained' scientific method, and certainly the notion – notably associated with the Ratio Club - that the radar experience invariably spelt *information discourse*. Indeed, although radar 'recruits' appeared, for instance, as a significant, transformative agent in Chadarevian's study of British post-war biophysics/molecular biology, *Designs for Life,* it is much more common among historians to regard the Ratio Club as exemplifying the beneficial spillovers of the war into biological terrains.[792] The latter acquired fame as the British pendant to the Macy Cybernetics 'group' - envisioned as it indeed was as a small, informal group of people 'half neurophysiologists and half communication theory and ex-radar folk with biological leanings'.[793]

'Noise' in brains and machines, the human servo, memory, pattern recognition and even 'telepathy' belonged to the subjects repeatedly returned to at the Club's regular meetings.[794] Whether or not, as one Ratio-Clubber, William Ashby, famed author of *Design for a Brain* (1952), complained some years down the road, this was merely 'a social club of no scientific pretensions (though very pleasant for an evening's speculations about the Universe and All that)' need not concern us here.[795] These marginal scenes obscure much of the everyday banality radar-technology in fact had assumed for many. The story of ex-radar biologists can be framed in much more mundane and instructive ways. And systematicity will do the work: in the British context, more acutely perhaps than elsewhere

791 Bates to Grey Walter, 27 July 1949, BATES, B.1
792 Chadarevian (2002).
793 Cited is Bates to Pringle, 3 August 1949, BATES, B.1; and see Hayward (2001); Holland (2003); Boden (2006); Husbands and Holland (2008).
794 See 'Subjects for Discussion' (February 1950), B.5; Bates to Brasher, 6 July 1948, BATES, A.89; Good to Bates, 10 June 1951, BATES, B.10
795 Ashby to Young, 22 May 1952, YOUNG, F.2

(but not especially peculiar either) it was the - simple and brute - lack of skilled wireless personnel that resulted in the systematic recruitment of non-physical scientists into radar and similar work.

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'I can take anybody who has reasonable training and/or good experience in high frequency work', as Frederick Brundrett, a scientific advisor at the Admiralty, submitted in October 1940.[796] Himself a Cambridge educated mathematician, Brundrett, like many another, was busy chasing 'likely personnel'. This meant 'suitable men from any source available'.[797]

Britain faced impressive shortages indeed. The total 'deficiencies' at the research establishments alone Brundrett then estimated to be 60 laboratory assistants, 90 experimental assistants, 60 experimental officers, and 8 senior experimental officers.[798] One year later, the establishments' requests for staff in 'radio work' ('highly qualified scientists', 'radio engineers', 'scientific and technical assistants') totalled some 460. 1455 were then already employed.[799] These deficiencies were even more impressive when one considered that the bulk of wireless personnel wasn't needed for the purposes of research and development but 'production', 'site-planning', 'installation, line-up and calibration', 'observation', 'interpretation and display', 'analysis' and especially, 'maintenance'.[800]

In July 1941, for instance, *additional* requirements in 'radio maintenance personnel' for all services were estimated at 20,747 (another 11,939 being 'available or under training') With the ongoing expansion of activities in operational research as well, there were growing concerns as to the 'impossibility' of recruiting men with 'some knowledge in radio' especially.[801]

796 Brundrett to Fielding, 22 October 1940, LAB 8/873
797 Hankey, 'First interim report' (item V.), 25 October 1940, WO 32/10992; 'Memorandum' (Fielding), 1 November 1940, LAB 8/873
798 Brundrett to Fielding, 22 October 1940, LAB 8/873
799 'Statement on staff employed on radio work in the services', 9 June 1942, LAB 8/506
800 'Personnel for R.D.F.' (memorandum by Wattson-Watt), 28 April 1940, AVIA 9/36
801 'Navy, Army and Air Force requirements for radio maintenance personnel' (July 1941); Capon to

By then, a 'very large number of young men' had long been 'combed off' already: from the universities (notably by Brundrett), industry (which naturally balked at the request), and the GPO. These sources, Brundrett had surmised by the end of 1940, were now 'exhausted'.[802] Rather atypically, Huxley, Keynes, son David and a few other Cambridge physiologists had been channelled into Blackett's 'circus' by A.V. Hill himself. Hodgkin, no longer a student, meanwhile had dutifully 'filled in a form which [put him] on the Royal Society register of scientists' (whose chairman Hill was as well). In October 1939 he had been allocated for work on aviation physiology. Hodgkin was interviewed by the Admiralty still in the same month. It was, however, a 'pleasant evening [spent] at the Hills' early in 1940 that ultimately decided his wireless fate.[803]

There were 'so many people at present taking action in regard to wireless personnel', the chairman of the electrical engineering sub-committee of the Scientific Register noted towards the end of 1940, that more coordination among the various parties seemed mandatory.[804] In the face of these numbers, officials at the Ministry of Labour now resorted to the position of supplying 'material for training' rather than 'trained material'.[805] The only way to meet these demands, as the chemist-novelist C.P. Snow, then a civil servant at the Ministry of Labour (one of those busy recruiting candidates), remembered later, was to 'manufacture' these people.[806] And manufacture they did. The so-called *Wireless Personnel Joint Committee* was appointed in January 1941 under Lord Hankey and charged with 'co-ordinat[ing] the demands' in matters of 'skilled and semi-skilled' wireless personnel generally, and with devising and implementing 'wireless training schemes' in particular.[807] The 'fullest possible cooperation' of universities and

Clement Jones, 30 April 1942, LAB 8/506

802 Brundrett to Fielding, 22 October 1940, LAB 8/873; and see Pringle and Peters (1975): pp.537-538.

803 Letters to mother, 31 August 1939; 13 October 1939; 11 January 1949; in HDGKN A.142

804 'Memorandum' (by Fielding), 1 November 1940, LAB 8/873

805 'Supply of Wireless Personnel' (memorandum 30 November 1940), LAB 8/873

806 Snow to Roskill, 6 January 1974, Hankey papers, HNKY 12/1

807 See minutes of 2nd meeting, 11 February 1941, LAB 8/522

technical colleges was promptly secured.[808] For the young people more or less suitably inclined, special syllabi were drawn up to give science courses at the universities a 'definite radio bias'; 'intensive summer courses' were launched; and from mid-1941 a scheme of 'state bursaries' was in operation to assist these diverted students. 'I suggest that persuasion in the direction of physics is now justified', C.P. Snow reviewed the progress in mid-1941:

> I do not mean any sort of coercion, nor doing violence to a man's genuine inclinations; but I do consider without any qualifications that a young man now on the point of e.g. reading mathematics, can properly be told that he will be more valuable to the country if he changes his university course to physics.[809]

By the end of 1941, the Treasury had granted £60,000 in support of 'wireless training for young people'. 11,969 young men were 'in actual training' in 85 technical colleges ('ab initio'), in addition to the more advanced training offered at the several specialised radio schools. The universities, meanwhile, were charged with the target of supplying 500 radio-skilled final year students by the end of the year – a sixth of the entire science student population graduating in 1941.[810] Later in the year, the scheme, soon underway at all the major universities, was fixed at the new target of 1,000 university students annually, supplied on the basis of extended, two-year radio courses.[811] Half of them were to be drawn from category 'A': students of 'physics and light electrical engineering'; the rest, from category 'B': 'students of other scientific subjects'. In each case, 'as much emphasis as possible' was to be put on the 'electrical aspects' of their curricula.[812]

Snow took it upon himself to tour the universities and select the 'suitable boys'. By March 1941, Snow had seen 'just over 1,000 undergraduates' already. Snow made it a point

[808] 'Provision of Skilled Radio Personnel' (minutes of a meeting on 21 November 1940), LAB 8/873

[809] 'War Cabinet. Skilled Radio Personnel. Second Progress Report', 1941, WO 31/10992; Snow, 'Hankey Radio Training Scheme', Report 1, March 1941, LAB 8/873; and see 'The intensive training scheme' (March 1942), p.2, copy in Hankey papers, HNKY 12/1

[810] See minutes 11 February 1941, LAB 8/522; 'Hankey Radio Training Scheme', Report 3, (July 1941), LAB 8/873; 'Wireless Personnel Joint Sub-Committee', Minutes 7 July 1942, LAB 8/506; 'Training for Radio Personnel' (1941), LAB 8/506; 'Returns from Technical Colleges' (September 1941), LAB 8/506; and Appendix VII, 'Provision of Skilled Wireless Personnel', Minutes 9 June 1942, LAB 8/506

[811] 'University Radio Syllabus 1942-43', Report April 1943; Appendix 'State Bursaries' to Interim Report (1941); minutes 17 June 1941; 18 November 1941; LAB 8/506

[812] Snow, 'Hankey Radio Training Scheme', Report 1, March 1941, LAB 8/873

to individually inspect each potential candidate: '[W]e tried to explore the man's general scientific ability, his experimental sense, his aptitude for radio, and his personality'.[813] Of the 650 students Snow actually recruited in 1941, eleven students came from classics, geography, law, modern languages, economics, and geology. Thirty-one were engineers, thirty were biologists, and an additional sixty-seven were students of chemistry. In terms of category 'B' men, thirty may seem a low figure - it amounted to about a third of all the men enrolled in biological subjects.[814] These figures would remain roughly constant until end of the war.[815]

We can, then, form a good impression of the scale of this intervention, which rendered electronics into something much more mundane – for many. The nature of these electronic conversions will be explored in detail below. It would require a very different thesis and approach to arrive at definite conclusions as regards the general impact of these measures. The present argument is indeed concerned with something else: dispelling the notion of radar as high technology, and making sense of the notion of a mundane, electronic world. Here is not the place to explore how profoundly these assistants, engineers and specialists went on to shape the spaces we historically identify as biophysics, cybernetics, medicine or physiology. There is every reason to assume they did shape them, profoundly and pervasively. From the late 1940s, for instance, small electronics firms mushroomed, pushing also into the biomedical market; technical manuals and reference texts such as *Medical Electronics* (1953) or *Electrophysiological Technique* (1950) now abounded and concentrated the new wisdom - with countless acknowledgements to now obscure firms, nameless 'electronic assistants' and unknown engineers such as Mr Dickinson, B.Sc., author of the *Technique* and himself of electronic assistance to the Oxford physiology department.[816]

813 Ibid.
814 In addition, the 1941 recruits were composed of 188 physicists, 191 electrical engineers, and 158 mathematicians.
815 Bragg to Lindley, 17 April 1945; 'Note to Mr Holye', 15 June 1945, LAB 8/ 1645
816 Dickinson (1950); Donovan (1953).

A new profession of 'biomedical engineers' promptly coalesced in the 1950s, complete with journals, societies and 'task forces' meant to draw together, as the first editorial of *Medical Electronics* read, at 'horizontal, trans-, and inter-discipline level' all this electronic knowledge 'now scattered'.[817] 'There must be instrumentation specialists … at home in applying their resources to biological problems', as nerve-biophysicist Schmitt submitted on behalf of the NIH 'task force' Bio-medical Instrumentation in 1956.[818] The following will return us to war-time electronics rather than tracing its consequences. But, we may imagine, here was also being created the human, faceless substrate that tended, built, designed, looked after, helped-out, invented, maintained, repaired, and would keep it going, the new electronic world of biophysics.

At home in an Electronic World

Conversion - 'drastic re-orientation' - was the systematic experience of the radio-war.[819] It was a matter of scale, as we have already seen. But as such, it was one of *kind.* Only after entering these establishments of secret science, as Alan, the fictional hero of *Glide Path*, recorded, did he have to say 'good-bye to the simple, old-fashioned world of "wireless"'; he was coming 'face to face with the unsuspected marvels of radar.'[820]

We know very little, in fact, about these putative marvels in their own right. Qualitatively, radar meant a different type of doing electronics - conceptually, institutionally, and materially – but the many, technical histories tend to be silent on such matters.[821] Historians of science, meanwhile, have engaged with physics and its

817 E.g. Schwan (1991); and see nn. (1963a); Rémond (1963).
818 'Instrumentation in Biomedical Research', MC154, Box 20, Folder 29
819 'War Cabinet. Skilled Radio Personnel. Second Progress Report', 1941, WO 31/10992; Snow, 'Hankey Radio Training Scheme', Report 1, March 1941, LAB 8/873; 'The intensive training scheme' (March 1942), p.2, copy in Hankey papers, HNKY 12/1
820 A.C. Clarke (1970): pp.25-26.
821 On the purely technical aspects, see any one of the technical histories; these abound - e.g. R.A. Smith (1947); Reuter (1971); Rawlinson (1985); D.M. Robinson (1983).

transmutations (or perversions) *through* electronics - 'device physics' - less the electronics themselves.[822] But even so, we can make some sense of these transformations - in the way they interest us, in connection with the ongoing, increasing *resolution* of the cell's bioelectrical substrate. Not any technological or scientific development in particular will matter, but the many and multiple, small and mundane transformations. As one war-time radar teacher surmised in 1943, the establishments were quite different 'surroundings'; and operating in them meant a particular 'frame of mind'.[823]

These, after all, were no 'average' *communities.* Male, secretive, neither civilian nor service, academic rank and social class losing their marks of distinction, their inhabitants existed in a somewhat liminal state, developing peculiar 'languages' and rituals, as we already know. Here, the normal order of things was suspended: '[A]ll scientific and technical staff', Rowe let it be known at TRE in 1940, 'must be here on Sundays and ... rest times must be taken on other days'.[824] The 'business of teaching radio', too, was 'so new an art' that 'in such an advancing science the lecturers [found] it difficult to keep pace'.[825]

One had to deal now with unprecedented *numbers* of those to be initiated – and a certain amount of logistics: implementing the scheme left its palpable traces in the academic landscape. It meant supplying university laboratories with 'enough radio apparatus to cope with a thorough experimental course' in ways that ensured optimum results for the services.[826] The equipment, 'more up-to-date' than university men had 'anticipated', was also less hodge-podge than the electrical things one had known. Precious 'unit sets' of the latest valves, resistances, transformers, chokes, beat tone oscillators, cathode ray tubes, single and double-beam oscilloscopes made their way into academia, and even larger quantities of such 'special equipment' swamped the technical colleges.[827]

[822] See especially Forman (1987); Forman (1996); Bromberg (2006).
[823] 'University Radio Syllabus 1942-43', Report April 13 1943, LAB 8/506
[824] Note by Rowe, 25 November 1940, AVIA 7/2746
[825] Snow, 'Interim Report' (December 1941), LAB 8/506; Browne to Hankey, 8 April 1942, HNKY 12/1
[826] Snow, 'Hankey Radio Training Scheme', Report 1, March 1941, LAB 8/873; Wilson to Hankey, 19 August 1941, LAB 8/506
[827] 'Equipment ordered for technical colleges', 'Equipment ordered for universities' (23 February 1942),

Here was engineered the conversion of university laboratories and work-shops into nurseries of electronic war, a process eventually superseded by the 'reconstruction' of academia by means of surplus: miniature, combative radar stations. By the end of 1947, the University Grants Committee will have spent more than £300,000 on such objects, stuff and (by then) electronic *scrap*.[828] '[I]nsights into operational conditions and applications', as a Professor Carroll of Aberdeen still submitted in 1942, 'should serve as a most useful guide to University Radio Teachers'. The 'appropriate emphasis' would be helped by the dissemination of 'Service Circuit Diagrams'.[829]

Uniformity and military encroachment, naturally, had consequences for what was taught and how in terms of electrical science. It resulted in a tremendous bias towards practical things, for one, and even only a sub-set thereof: amplifiers, oscillators, transmission lines, pulsed circuits, measurement, aerials and radiation were considered the 'essential' topics-to-be-covered, together with the 'mathematics as are necessary taught in a manner specially devised to meet the needs of these students.'[830] At TRE, too, classes were heavily slanted towards electronic practice: '50%' would be devoted to 'circuits &c.', the eventual TRE *Teaching Panel* resolved, and another 40% to aerials, lines, waveguides, and 'equipments': initiation to 'the atmosphere of TRE'.[831]

This meant learning to think *with* rather than *about* things. Rather than the advanced, abstract secrets of servo-theory or signal transmission then under development, here was instilled what we have already encountered as 'the production outlook': teaching the novice 'what can be made and what can be made most easily'.[832] The exams questions ('SECRET') students were confronted with at A.A. Radio School, for instance, typically

LAB 8/506

828 HMSO (1948): p.22.

829 'University Radio Syllabus 1942-43', Report April 13 1943; Convention of University Radio Teachers, Minutes of Syllabus Sub-Committee, 14 April 1942; and see 'Teaching Syllabus in Radio Communication Course', LAB 8/506

830 Ibid.

831 TRE Teaching Panel, record of 3rd meeting (15 March 1944), BL 7.1

832 'University Radio Syllabus 1942-43', Report April 13 1943, LAB 8/506

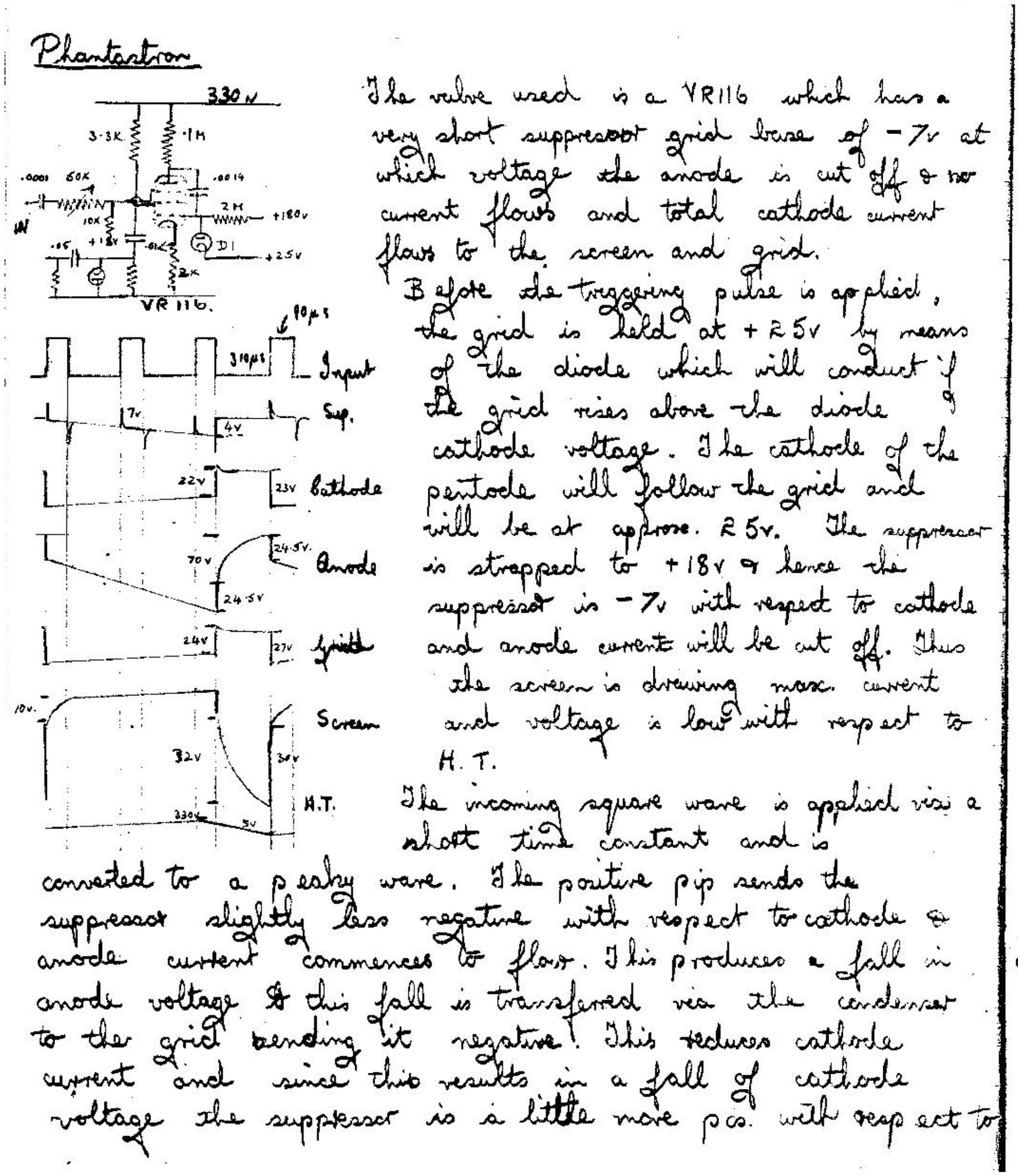
embraced items such as 'Draw a circuit diagram of a voltage doubler and explain the action', 'Why is it impractical to use standard types of valves and tuned circuits at centimetre wavelengths?', or 'What method of using gain and intensity control would you recommend to an observer to enable him to obtain the best results?'[833]

The corresponding mathematical 'needs', we know already, were practical rather than theoretical. And these needs were better served with the appropriate 'economy in training time', as physicist Ratcliffe announced. 'It was very important that the methods of thought should not be mathematical but should be along the lines of a physical explanation'.[834] As head of the A.A. Radio School, he took a special pedagogical interest in the matter.

Rather than pondering the formal beauty of Maxwell's equations, one would have resorted to such 'principle[s] of models' as Hodgkin too had mobilized when designing his radiation-patterns.[835] The 'lines of physical explanation' Ratcliffe had in mind here, not least, included circuit representations - even if circuits and their representations were not quite the same again. It was a visual language whose primary uses now definitely flipped from *representing structure* to *designing function* as historian Jones-Imhotep has argued: even less *indexical* and *map-like* - but more standardized - they answered to the new demands that were being made on them: precision, reliability, performance.[836] Consequently, one was better informed about principles of *designability*, a term coined at the time by F.C. Williams, the most reputed circuit wizard of TRE. Hodgkin, incidentally, often took Williams along in his car on their many sojourns to Manchester. But it is not the car-rides that should impress us. It is these barely perceptible shifts in the material life of circuits.[837] The figure below reproduces the *Phantastron*, one of Williams' notable creations, as it reappeared on

833 'Secret', loose sheet in Notebook no.6, WILKINSON
834 'University Radio Syllabus 1942-43', Report April 13 1943, LAB 8/506
835 'Preliminary Report on the Production of Narrow Beams', 13 August 1940, TRE REF 4/4/217, copy in BL 4, file 3
836 Jones-Imhotep (2008).
837 Jones-Imhotep (2008): esp.p.77; e.g. Hodgkin to mother, 13 May 1941, HDGKN, A.146; Hodgkin (1992): esp. p.170.

the pages of a radar novice's notebook:


Phantastron

The valve used is a VR116 which has a very short suppressor grid base of −7v at which voltage the anode is cut off & no current flows and total cathode current flows to the screen and grid.

Before the triggering pulse is applied, the grid is held at +25v by means of the diode which will conduct if the grid rises above the diode cathode voltage. The cathode of the pentode will follow the grid and will be at approx. 25v. The suppressor is strapped to +18v & hence the suppressor is −7v with respect to cathode and anode current will be cut off. Thus the screen is drawing max. current and voltage is low with respect to H. T.

The incoming square wave is applied via a short time constant and is converted to a peaky wave. The positive pip sends the suppressor slightly less negative with respect to cathode & anode current commences to flow. This produces a fall in anode voltage & this fall is transferred via the condenser to the grid sending it negative. This reduces cathode current and since this results in a fall of cathode voltage the suppressor is a little more pos. with respect to

Figure 50: 'Phantastron', c.1943

Almost like in a biology school book, in the upper left, artfully labelled in service standard nomenclature, is depicted the circuit itself, its looks; below, we find its responses, in diagrammatic form, to a pulsed input, and on the right, in verbose detail is rehearsed an account of its behaviours: so many layers of an electronic world, here serving to inculcate subtle shifts in the ontology and *practical* meanings of circuitry. Contemporary eyes would have been less prone to see in this circuit representation merely an electrical *structure* – or in that of a nerve or some other gadget - but the specification of a function, or process: a series of events.

This will be one of the subtle differences that distinguished the 'theoretical membrane' of our ex-radar biologists from the circuit morphologies – analytical structures - of the interwar period. And more generally, moving towards a thicker description of this radio-war and the historical changes it catalysed, gives a much richer sense of how cellular behaviour too would be resolved into a novel, electronics-mediated space of electrical micro-dimensions. This space would no longer contain the impulse as the 'atomic event' or the 'propagated disturbance' that was still celebrated as such by the likes of Hill and Adrian twenty years earlier.[838] The decomposed impulse and its model would become persuasively *real* in the midst of such things as circuits-as-functions, modeling strategies, and a great many electronic things.

These new levels of resolution, and the *decomposition* which we will find reflected in the bio-electrical imagination as well, were not least palpably material: *embodied in* these novel things rather than merely *uncovered by them.* Gradually, the terms in which this electronic world had to be imagined had become one of the internal micro-morphologies of things electrical, and the micro-temporalities of electrical processes. The historian Hintz has shown how the history of electronic miniaturization then set in with such mundane, ubiquitous and crucial electrical objects as batteries – portable power for portable devices - and not, as one might think, in 1948, with the iconic *transistor*.[839] Miniaturization was one dimension, conceptual *depth* another: 'even the shortest piece of connecting wire was no longer just a piece of connecting wire but in itself a tuned circuit' as one diverted Post

[838] E.g. A.V. Hill (1932a); Adrian (1928).
[839] Hintz (2008).

Office engineer would reminisce.[840] Inconspicuous items such as cables – now 'coaxial' - weren't the simple and homogeneous, perhaps insulated, bodies any longer. Their newly complex anatomy was something still to be digested - again, here as duly recorded in novices' laboratory notebooks:[841]

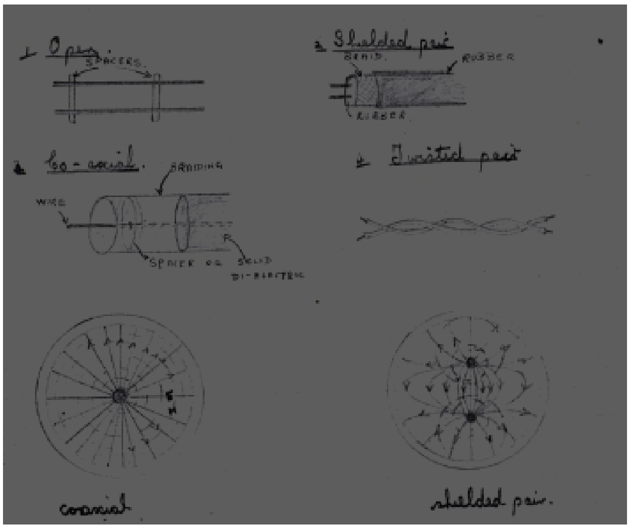


Figure 51: The anatomy of cables, c.1943

These sea-changes, to be sure, had been longer in the making. 'In the last 15 years', as *Popular Science* informed in 1946, vacuum tubes had 'gone far afield from their original uses in communication to become the valves, triggers, and throttles of modern industry.' But it was with radar, the piece opined, that the micro-dimensions, the 'behaviour' of electrons 'during … microseconds' and wave lengths 'comparable with the size of the tube', became 'vitally important to performance.'[842]

It became evident that 'a totally new kind of thinking' became necessary. As things changed, and the demands made on them, so did the 'kind of thinking'. This material basis of this progress story, as the article quite rightly points out, was modern industry, and domains such as control and telephone engineering.[843] *Performance* drove things onwards:

840 Latham and Stobbs (eds.) (1999): p.145.
841 Source: Notebook no.3, p.14, WILKINSON; on the quite different nature of wiring previously, see Mellanby (1957).
842 Vogel (1946): p.16.
843 Vogel (1946): p.16; Hagemeyer (1979); Bennett (1993); Mindell (2002).

'No longer could the tube be considered merely as the electronic component of a circuit composed of conventional inductances, capacitors and resistances.' It was certainly no coincidence when in 1958 the philosopher of technology Gilbert Simondon developed his 'phenomenology' of the progressive 'concretization' of the 'technical object' (*as such*) on the basis of a veritable natural history of the vacuum tube - collected, arranged chronologically, labelled and photographed: 'The successive precisions' the tube underwent, Simondon mused, involved its 'indistinct structure corresponding to ionization [being] wholly replaced by the thermoelectronic characteristic'. The tube, once an 'artisanal object', by 1958 had turned into an 'axiomatic system'.[844]

Whatever we make of Simondon's idea of technological 'evolution', in its phenomenological ambitions it usefully captures the sense in which the ways of knowing, handling and seeing electrical *behaviour* were subject to change. In only a short few years, these material micro-manifestations of electricity expanded from fragmentary beginnings and scattered islands of the electronic arts into something much more present, pervasive, and much more palpable for many: a manufacture of things and people. This electronic world in-the-making was multifaceted, material rather than disembodied, and more often than not, as we have seen, banal and less than futuristic. And this, accordingly, was the *world* and not so much the *context* wherein we have to imagine the postwar biophysics of nerve taking shape. The action potential too would become manifest, resolved, and modelled in a novel world of electrical micro-dimensions.

[844] Simondon (1958): pp.26-30.

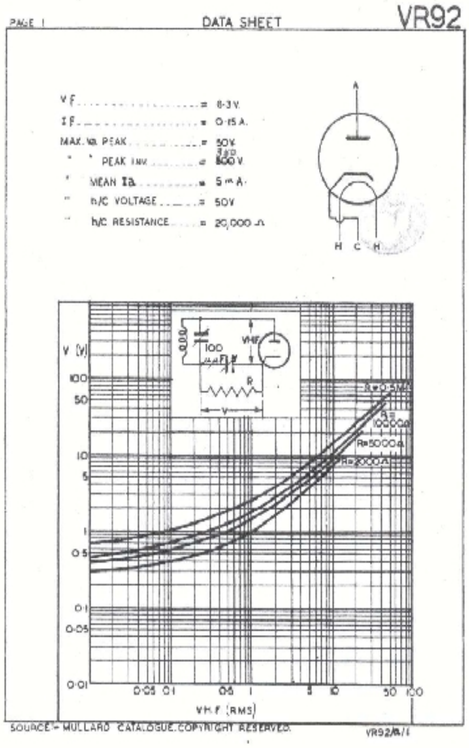


Figure 52: VR92 valve data sheet, c.1945

Transferred

'Calculators (Hand operated)', 'Calculators (Electric Semi-Automatic)', 'photographic equipment', 'Communications Equipment' (transmitters, ground transmitters, airborne transmitters, receivers, combined transmitter-receivers), 'Electrical Meters', 'Miscellaneous Electrical Equipment', 'Radio Test Equipment' (Test Set Type 218 ... Type 237A ... 1117 ... Wavemeter Type 1409 ... Oscilloscope Type 11 10SB/562 ... Control Unit ... Signal Generator Type 38 ... Type 47 ... Oscillators … Amplifying Unit), 'radio components and equipments' (condensers, resistors, potentiometers, switches, valve holders, pentodes, triodes, diodes, tetrodes, rectifiers, control tubes, ray tubes, photo-cells, wire, cables, plugs and sockets).[845]

So read the lists Alan Hodgkin studied in the summer of 1945: War-machinery turned surplus; endless lists of things, big and small, more or less useless now, piled up in government surplus stores. The 'nation ha[d], in fact, become instrument-minded', one read in *Nature*, turning scrap to good use as it was now 'confronted with its post-war problems'.[846] Hodgkin, in this summer, ordered for himself (among many other things) six oscilloscopes type 10, two control units type 409, a test set type 37 (beat frequency oscillator), and eight cathode ray tubes – four each of models VCR 97 and 517 respectively: 'Blue Screen' and 'Blue flash Yellow afterglow'.

In addition, 'experimental' Geiger counters from new friends at GEC, oscillographs from Cossor, and amplifiers from the all-too familiar TRE laboratories soon made their

[845] See lists of surplus equipment in HDGKN B.321; B.322
[846] nn. (1943): pp.704-705

way to Cambridge.[847] And Hodgkin had long stock-piled circuit diagrams (when of 'extremely good design'), 'data sheets', 'test gear', and TRE 'stock lists'.[848]

Returning academic war-recruits never *returned*, in more than one sense. As masses of electronic scrap and instrumentation, machine tools, war booty, 'electronic assistants' and other useful items were flowing into the post-war world of academia, one was, as one somewhat frustrated scientist in charge of such redistribution recorded, in most instances 'not dealing with an <u>enumerable</u> set of objects'.[849] The biophysical spaces that were taking shape here we should not imagine as laboratories being now populated with elaborate electron microscopes, x-ray diffraction equipment, or scintillation counters. There were, primarily perhaps, a matter of less perceptible, mundane material transformations.

When Hodgkin's future collaborator Katz returned to England in 1946, he found himself re-settling in London amidst electronic scrap, left-over rubble and an ambitiously reconstructing college where it was decided that '[i]ndeed it is especially on the border line between two formerly separated sciences that the most productive fields of research lie'.[850] At UCL as elsewhere, a 'great variety of electrical apparatus' was purchased from government surplus stores; co-operations planned; 'rehabilitation' funds secured; more 'suitable people' recruited - or re-recruited, like the young, electronics-savvy Keith Copeland of T.R.E. or Hill's time-honoured assistant Parkinson who had spent the war-years in the work-shops of Farnborough (and now was doing 'great work in the acquisition of a great deal of valuable equipment at very low prices').[851] Hodgkin, too, upon his return scouted for 'electronic assistants' among his former TRE colleagues: people such as M.G. Harris, born 1922: 'entry into TRE 25/10/43', as Hodgkin noted, 'reasonably intelligent';

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847 Hodgkin to GEC, 17 October 1946, HDGKN H.28; Adrian to Cossor, 15 May 1946, HDGKN H.27 ; Taylor to Adrian, 5 March 1947, HDGKN H.29

848 Hodgkin to Sturdy, 24 February 1944; Hodgkin to Rushton, 25 February 1944, A .170

849 Bullard to Chesterman, 13 July 1945, AE/9/2; and see 'Minutes of Meeting' 5 November 1945, HDGKN B.322; Blackett to Egerton, 16 July 1945; Egerton to Treasury (draft letter, nd), AE/9/2; Bullard to Egerton, 29 September 1945, BLRD B.11; HMSO (1948): p.22.

850 'Memorandum on the Optimum Size', Appendix III, 7 May 1946, UCC 1945/1946

851 Pye to Dale, 15 July 1948, HD 6/2/9/1/74; also see Logan to de Montmorency, 12 July 1950, UGC 7/127 Paper F.43/7

or one E.G. Sanders who had entered TRE in June 1942 after four months of radar school: 'quite keen on the job ... refined accent.' Eventually, Hodgkin settled with R.H Cook, recruited from the Electrical Test Engineering Section of Pye Radio Ltd.: 'My hobbies are', Cook introduced himself, 'Television, Electrical Horology and Marine Zoology'.[852]

'It [was] a fact', the first report of the Joint-Committee on Biophysics (which was launched in 1947 by the Board of the Faculty of Science at the University of London) diagnosed, 'that owing to the war, many young people with a good knowledge in technical physics are at present available'.[853] Some 70 diverted students plus teaching and research staff were to make it back - 'made available again' for academic research - to the Cavendish Laboratory alone.[854] Roughly two thousand young men 'competent to undertake pure research' were expected to resume their interrupted academic lives in 1945 (in all the natural sciences and all universities). The post-war reconstruction programme of the Royal Society, engineered, notably, by Hill and Blackett, very strategically converged on the 'borderlines between the sciences'. In parts, the programme like a rehabilitation-plan for these diverted, no longer easily-classifiable men: biophysics, oceanography, radiology, geophysics, certain 'electromechanical contrivances' (computers), and radio-astronomy were singled out as the 'ventures which would benefit the progress of science', as President Sir Henry Dale had it.[855] Among these returnees, of course, was a 'number of able, young biologists [who had] gained ... an extensive knowledge of practical physics'. As A.V. Hill gathered, an 'important new development' was on the horizon.[856]

Always a man of action, Hill himself promptly launched a small re-education project for three young radar scientists. They 'always wanted to do medicine' but had

852 Cook to Hodgkin, 18 February 1948, HDGKN B. 149; and see notes (ca. 1945) in HDGKN B.323
853 Report of the Joint Committee on Biophysics, undated (1948), RNDL 2/2/1
854 Memo by Gunn, 19 April 1945, LAB 8/1645
855 Royal Society (1945): esp. p.15; Dale to Anderson, 8 March 1945; Egerton to Proctor, 8 May 1946, T161/1201; also see A.V. Hill and Munro Fox (1946).
856 Memo to Lindley, 17 April 1945, LAB 8/1645; Hill to Dale, 3 March 1945, HD/6/8/6/5/192; and Hill to Merton, 12 June 1944, HD/6/8/6/5/168

obtained a State Bursary for radar training instead - 'prevented', as Hill said, from following their 'more natural bent'.[857] 'After having been so soaked in physics' during the war, they had to 'pick up the other side by just as deliberate soaking', Hill explained. As a first countermeasure, Hill sent his recruits - (later Sir) E.J. Denton, J.M. Ritchie and B.C. Abbott - 'all off to Plymouth'.[858] The grand scheme was a 'beach-head' for biophysics: to get going again at UCL, after six years distractions and destruction, 'a good strong, viable organism of biophysics'.[859] Being an ex-radar man, Bernard Katz 'would be able to speak the … [right] language', Hill strategized, and serve as his 'senior lieutenant'.[860]

These were the ways that the post-war world of cellular behaviour was *crafted*. Behind these new landscapes operated processes that were much more strategically, deliberately and ideologically charged than any talk of technological *diffusion* or the *migration* of skills, tacit or otherwise, might suggest. *Transfer,* in particular, was a word and an issue deeply on the minds of actors, whether recruiting 'electronic assistants', buying electronic surplus scrap or starting new scientific ventures. In England, in particular, such transfer-mindedness was deeply embedded, like the ex-radar persona himself, in the war-time ideology of the people's war, of dissolving barriers and crossing boundaries, and of muddling through and 'mixing up' - between social classes; between specialities; between academia, government and industry. *Transfer*, reconstruction, and the creation of scientific borderlands were issues intimately linked.[861]

The 'Transfer method in research' was after all, as a 1950 student-guide in the *Art of Scientific Investigation* informed, 'probably the most fruitful and easiest method in research'. Penned by the Cambridge Professor of Animal Pathology - until recently engaged in a war-time project concerning the production of virus vaccines - here one learnt that in science,

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[857] Application by A.V. Hill, 5 April 1946, FD 1/5105

[858] Hill to Havelock, 25 May 1954, AVHL II 4/35; Hill to Denton, 30 August 1948, AVHL II 4/20; Hill to Mellanby, 10 November 1947, FD 1/5105

[859] Hill to Merton, 12 June 1944, HD/6/8/6/5/168; Hill, letter draft, 9 November 1945, MDA A8.32; and see Faculty of Medical Sciences, UCL Development Plans, Report No.1 (1950), UCC 1949/1950

[860] Hill, 'The Need for an Assistant Director' (September 1945), AVHL II 4/46

[861] Calder (1969); Rose (2004): chapter 2.

'every useful stratagem must be used.'[862] Such transfer of methods distinguished, famously, the operational researcher, and much more generally, *transfer* was a category central to the anthropology of total war. 'Transfer of training and skills' was a process studied and theorized in the laboratories of applied psychologists - for instance, at Cambridge, where the training of 'radar operators' emerged as a favourite subject of study.[863] In moving pictures such as the Ministry of Information short *Transfer of Skills* (1940), the subject had been broadcast to the population at large: Craftsmen of peace-time transferred their special skills to problems essential to war production – makers of luxury pocket-watches transformed into makers of bomb-fuzes, fishermen knitted nets not for the purposes of fishing, but of the kind required to camouflage weapons and factories.

In the post-war period, migration of concepts, methods and tools did not spell violation, but promise, and progress. The biological war-returnees, too, young, research-minded, having tasted organized and collaborative science, returned envisioning a distinctive form of biological science. At issue was not the creation of a new discipline, but rather, an attitude and frame of mind: quantitative, fundamental research - borderland work. A 'happy combination of medical graduates, physicists, engineers and mathematicians' as Katz envisioned it.[864] 'Need for breaking away from the conservatism of <u>farmer</u> and <u>doctor</u>,' as Hodgkin would dutifully excerpt from Bernal's *Science for Peace and Socialism* (1949): 'Basic research ... Reorganization of the biological sciences on functional basis.'[865]

Still in late 1945, the launch of the discoverer of the squid giant axon J.Z. Young onto the vacant UCL anatomy chair had sent shock-waves through the British medical

862 Beveridge (1950): p.129.
863 E.g. Mackworth (1948); Lincoln and K.U. Smith (1951).
864 'Suggestions for the Organization of Research', (March 1945), copy in AVHL II 4/46
865 'Synopsis' (undated note), in HDGKN H.13

establishment. It was the first British anatomy chair to be 'handed over' to a man 'not medically qualified' the outcry in the *Lancet* went. Another 'tremendous asset to the place', Hill opined.[866] Young lost no time in staffing his scandalous department with a 'team' of electro-physiologists, histologists, zoologists as well as an electronic engineer from the Heston Aerodrome – all 'gradually losing their identity in this project' as Young approvingly observed by 1951.[867]

These people were out for reform, not a revolution, epistemic, disciplinary or otherwise. In the biophysical borderlands of nerve, brand-new, large and lavishly funded institutes such as Schmitt's Biophysics Laboratories at MIT (which made Hill 'feel quite jealous'), though featuring prominently in Rasmussen's *Picture Control,* remained the exception.[868] Spurred by electronics, the electro-physiology of nerve was moving apace, but expanding *within* existing institutional structures – physiology departments - not toppling over the extant disciplinary order.[869] Harvard, Johns Hopkins, MIT, Chicago, Columbia University, the Rockefeller Institute, Cambridge, UCL, Melbourne, Copenhagen, Uppsala, Stockholm, Berne, Paris, Kiel, and Freiburg were all moving, or moving deeper, into electro-physiological terrains and its borderlands.[870]

The world's new fabric, in short, was congenial to Hodgkin and fellow returnees and the project they had embarked upon: the physical aspects of the excitable cell. But these developments must be understood as intensifications not incisions. Certainly the ontological departures routinely associated with cybernetics - matter and energy into information, or the blurring of categories such as artificial and natural, or man, human and machine - obscure much of these far less discursive re-workings of the world. The Ratio

[866] Best to Hill, 26 October 1944, HD/8/6/5/174; Hill to Gasser, 1 March 1946, AVHL I 3/22; and see Young to Eccles, 29 November 1945, YOUNG, 90/1; and Brash and et al (1945).

[867] See Young to Wiener, 28 November 1951, MC22, Box 10, Folder 143; also see Roberts to Wiener, 17 January 1950, MC22, Box 7, Folder 110; Application by J.Z. Young, 11 January 1946, FD 1/3677

[868] Quoted is Hill to Schmitt, nd (1945), MDA A8.2; and see Rasmussen (1997a): chapter 4; also see in this connection, Wilson and Lancelot (2008).

[869] See Talbot, 'Bio-physics in Europe' (April 1957), copy in MC154, Box 21, Folder 10

[870] There is hardly much literature on these developments, but see Veith (ed.) (1954); Gerard (1958); Harrison (2000); Gruesser, Kapp, and Gruesser-Cornehls (2005); Schoenfeld (2006); more generally, see Cozzens (1997).

Clubs at best provided one part of the spectrum. At the other, such an established borderlands-venue as the Colloid Committee of the Faraday Society was reconstituted in 1948 as the Colloid and Biophysics Committee with representatives from bodies ranging from the Physiological Society to the British Rubber, Oil and Colour and the Cotton Industries Research Associations. The initiative to 'strengthen [its] biological side' was impelled by the likes of Rideal, Roughton, and Danielli who brought on board for these purposes new faces such as Hodgkin or physicist John Randall.[871] It carried forward a borderland agenda grounded in useful things, instrumentation and practices rather than an intellectual programme, let alone, an information discourse: 'Transpiration in Plants', 'Lipo-Proteins', 'Optical Methods for the Investigation of Cell Structures', the 'Electric Double-Layer', 'Fibre Structure in Biological Systems' or 'Polyelectrolytes and Detergents' belonged to the subjects chosen for its first few such gatherings in 1949-1952.[872]

In this world, as we shall see now, bioelectrical phenomena would become manifest in new and quite concrete, material ways: measured more often, more precisely, more easily. 'Provision' had to be 'on a scale ample enough to take full advantage of the new techniques' as E.D. Adrian submitted as he forwarded Hodgkin's future programme to the Rockefeller Foundation.[873] Its central 'problem', Hodgkin had written, would be the 'mechanism of transmission and initiation of the nervous impulse'. Electronic equipment, internal electrodes and single nerve fibres were the techniques to be developed, and as a novel supplement, Hodgkin's programme emphasized the 'use of radio-active tracers'. In this connection 'the general aim would be', as he explained, 'to keep a continuous track on

[871] See minutes of meetings 8 December 1948; 12 May 1949; 27 October 1949; Minutes of the Colloid and Biophysics Committee, RI; F.C. Tompkins to Hodgkin, 24 November 1948, HDGKN H.13; Roughton to A.V. Hill, 19 November 1948, ROUGHTON/CUL, Folder 20.78

[872] Minutes, 8 December 1948, Minutes of the Colloid and Biophysics Committee, RSC

[873] Adrian to O'Brien, 6 August 1945; and see excerpts from Gregg's diary, 20 September 1945; 16 November 1945; RF/RG.1.2, 401 A, Box 13, Folder 114; also see Adrian to the MRC, 13 February 1946, FD 1/4651

the movements of ions into and out of cells.'[874]

Next to electronics and numerical practices, here was yet another, substantial layer of this newly quantitative, bioelectrical world: tracers. Thrown into relief by tracer elements, together they would fundamentally shape the ontology of post-war cellular behaviour.

The world resolved

Beginning in 1946, £3,000 annually crossed the Atlantic in order to get the biophysics team started.[875] Squid tanks would have to be repaired (the one at Plymouth having suffered severe bomb damage), isotopes procured, a 'team' assembled, new techniques taken fully advantage of.

Adrian had lost no time praising the brilliant conditions such 'research into the biophysics of nerve' would meet in Cambridge, skilfully operating the registers of progressive science: Physiology had developed close relations with the Department of Colloid Science - experts on the 'chemistry of living surfaces'; and close relations had developed with the Biochemistry and the Cavendish Laboratories where various 'teams' dealt with protein structures and radio-active substances. The 'need for co-ordinated research on war problems', Adrian observed, 'had made this collaboration [between departments] even stronger.' Even more attractive, of course, was the presence of a number of men who had been 'diverted' to research on radar: they had the 'training, outlook, and ability to make a very strong research team indeed'. [876]

With them, we will zoom closer now into this new biophysical borderland of

874 'Future Research on Physical Aspects' (September 1945), HDGKN H.1

875 Unit of Neurophysiology, RF Grant – Expenditure and Estimate (1946-1947), HDGKN B.2; Adrian to RF, 7 January 1947; Gregg to Adrian, 11 October 1947, RF/RG.1.2, 401 A, Box 13, Folder 114; Young to Hodgkin, 30 June 1947, YOUNG, 93/89

876 'Application for a Grant for Research into the Biophysics of Nerve...' (October 1945), RF/RG.1.2, 401 A, Box 13, Folder 114

numbers, models, and electronics. We have, in fact, already seen a great deal about how it had been in the making, expanding, and transforming, and here we will begin to inspect the bioelectrical micro-dimensions it opened up: the fabric from which the new model of nervous activity would be wrought. We begin with the things themselves: The present section will argue that even its core conceptual element, the 'sodium hypothesis' – on the face of it, an almost disappointingly unspectacular, low-tech development - emerged from this fabric. The hypothesis was a significant turning point in the story of the action potential *problem*. And it was a turning point because, as we shall see, the world, and thus, the substrate of cellular behaviour itself were transforming.

In the fall of 1945, this world still was very much under construction. There was, for instance, the 'worrying' 'question of getting squid in good condition'. 'The essence of the business', Young's most practical advice to Hodgkin went, was 'to get in the minds of the fishermen that what you need is one live squid, and not 500 dead ones!'[877] Special electronic equipment ordered from overseas was not properly delivered either, held back by customs regulations; isotopes and the all-essential re-construction of the aquaria - 'to keep the squids' - suffered delays as well. It was only in the course of 1947 that such items finally were 'beginning to materialize'.[878] Only gradually, things got rolling again. By the fall of 1946, a 'joint programme' had been underway between Katz and Cambridge.[879] And they started where they had left off – or almost.

In 1946, one was at best hovering on the brink of what would soon become a world resolved into its bioelectrical micro-temporalities. Silhouettes, however, of this other space were clearly taking shape, albeit still vaguely, and as far as the nerve impulse was concerned, still mostly on paper: Hodgkin's programme had a clear focus: It centred on

[877] Young to Hodgkin, 30 June 1947, YOUNG, 93/89

[878] Unit of Neurophysiology, RF Grant – Expenditure and Estimate (1946-1947), HDGKN B.2; Adrian to RF, 7 January 1947; Gregg to Adrian, 11 October 1947, RF/RG.1.2, 401 A, Box 13, Folder 114; Young to Hodgkin, 30 June 1947, YOUNG, 93/89

[879] Katz to Hodgkin, 20 December 1946; Katz to Hodgkin, 6 March 1947, HDGKN H.7; Hill to Gasser, 1 March 1946, AVHL I 3/22

ions – so as to account for the observed dynamics of the nerve potential; and in particular, it centred on two, most simple ionic species: potassium and sodium. 'I have not got much further with the prblem [sic]', Hodgkin jotted down in late 1946. 'The main things that we want to settle' concerned 1. the leakage of potassium 'per impulse', 2. the possibility that leaking potassium 'exchanged' with sodium, 3. how fast did radioactive potassium enter a resting axon, and 4., how fast did sodium enter an isolated nerve?[880]

That potassium made it on Hodgkin's list of things-to-settle is hardly surprising. Potassium, we know, had long been associated with bioelectrical potentials, even as preciously little was known about the temporal dimensions of such processes. Certainly nothing in the way of 'per impulse'. But not, sodium. Indeed, the appearance on Hodgkin's list of sodium was far less obvious and so was that of ions that *entered* the nerve during its explosive activities.

Quite the opposite: the idea of a substance being *lost* during activity was deeply ingrained in the minds of nerve-physiologists, enmeshed as it was with the 'classical' postulate of a membrane *breakdown*. 'The word, breakdown, suggests leakage', as Rudolf Höber still confidently declared in 1946.[881] Sodium, meanwhile, was practically non-existent in physiological terms. This despite the fact that as early as 1902 the botanist Ernest Overton had stumbled over the *Unentbehrlichkeit* of sodium for certain bioelectrical phenomena: muscle fibres ceased to contract when immersed in sodium-free solutions - after several hours.[882]

Worse, the very idea – sodium-permeability - found influential opponents. They were impressed not least by the potential 'oceanic significance' of potassium accumulation processes on 'paleaochemical' time-scales: a line of reasoning, as *un-impulse-like* as possible, according to which the 'origins' of intracellular potassium directly translated into the

880 Hodgkin to Cole, 17 October 1946, HDGKN D.96
881 Höber (1946): p. 386.
882 Overton (1902); Lorente de Nó (1947): pp.109-111; Hodgkin and Katz (1949): p.44.

evolving K/Na ratio of the ocean and categorically ruled out permeability of cellular membranes to sodium and other such 'larger' ions.[883] These were the 'arrangements', the acclaimed Irish muscle physiologist Conway argued in 1941, that clearly were 'of the greatest advantage to the cell' from osmotic and nutritive points of view.[884]

Sodium was both, not salient at all and too much so. Sodium was, after all, the major electrolytic constituent of sea-water – routinely used by physiologists as a bathing fluid for their preparations and as a stand-in for the cell's external medium. It routinely appeared on the balance-sheets physiologists drew up to calculate equilibrium potentials; so it did, certainly, on the sheets – ionic distributions - drawn up by Hodgkin at the time. His notes ominously made reference however to something else - some 'missing anion' 'X': X would be highly concentrated in the *inside* the cell, and occur in low concentration in the external fluid.[885] X would be a substance lost.

In terms of its ionic composition, this had been a world largely unknown, uncharted, and *un-labelled*. The 'difficulty of sodium micro-chemical methods' especially had done little to further the electrolyte physiology of sodium.[886] It was the substrate of the world, in short, that made it difficult to see a 'sodium hypothesis', let alone, to give it a quantitative formulation. But when sodium made its prominent appearance on Hodgkin's future programme, the ionic world-picture had already begun to move definitely, and broad-scale. And more than anything else, the 'hypothesis' (more on which shortly) was simply an articulation of a world resolved and traced by electronics and radioactive isotopes.

Indeed, if these tracers had not impressed the biological imagination already before the war, they belonged squarely to those 'strange applications' the war had 'thrown up', as A.V. Hill waxed enthusiastic.[887] Huxley's war-time room-mate, ADRDE officer and future

[883] E.J. Conway (1941a); on Conway, see Maizels (1969).
[884] Boyle and E.J. Conway (1941): p.1; E.J. Conway (1941b).
[885] E.g. Hodgkin, notebook 'General physiology', p.8 (undated ca. 1945), HDGKN C.69
[886] Manery and Bale (1941): p.215.
[887] Hill, 'The need for an Institute in Biophysics' (1945), HD/6/8/6/5/184

Harvard biophysicist Arthur Solomon, had explained it all in his little manifesto – to be published with Penguin – *Why Smash Atoms?* (1945).[888] It is a story well known to historians: Within a short few years, once rare species of artificial radioactivity would transform into a mass commodity of sorts, *labelled substances* turning into a presence, each occurrence signalled by the click of a Geiger-counter.[889]

By early 1951, some 50 radioactive isotope projects had been 'approved' by the Clinical Applications Sub-Committee of the new MRC Committee on Medical and Biological Applications of Nuclear Physics alone. Percolating outwards from the establishments of secret science, these peaceful by-products of nuclear science – iodine, potassium, chloride, sodium and many another ionic species - gradually reformatted not least, as Jean-Paul Gaudillière pointed out, the physiological imagination – and palpable realities, we should add - of processes:[890] substance exchange, permeation, diffusion, secretion, 'fluxes', and 'transport' resolved into novel spatio-temporal dimensions and coalesced around a newly penetrable world of *surfaces*: frog skin, kidney, digestive system, liver, skin, muscle, placenta, capillaries, lymphathics, nerve and less living things as well: artificial membranes, separation surfaces, and selective ion exchange materials. One couldn't discern progress so much, as one biophysicist complained by 1949, than a 'mass of experimental data'.[891]

Cellular phenomena began to appear in a different light, quite literally. To be sure, traceable phenomena tended to operate on the time-scales of dietary experiments, of cellular growth and accumulation, of tissues perceptibly swelling and shrinking – not nearly, that is, approaching the time-scale of the nervous impulse: a matter of microseconds. Unfortunately, the 'resolving power of the tracer methods is very poor', as

888 A.K. Solomon (1945); and see A.K. Solomon (1993): pp.110-111.
889 See esp. Rheinberger (2001); Creager (2002b); Kraft (2006); Creager (2006); Herran (2006); Gaudillière (2006).
890 Gaudillière (2006).
891 Teorell (1949b): pp. 545-546; and see E.J. Harris (1960): p.7;p.13.

Hodgkin still complained in 1952.[892] And yet - a mass of experimental data: for biomedical scientists equipped with Geiger-counters, days turned into hours, hours into seconds, statics into kinetics: gross balance sheets and de-territorialized concentration differences were displaced by exchange *rates*, equilibria gave way to dynamic steady states, electrolytes were being *localized*.

These were the new appearances of cellular life. Wallace Fenn, a sometime student of A.V. Hill's, now casually alerted the readers of the *Scientific American* to such items as: 'muscle seems to be permeable to sodium, as shown by experiments with a radioactive isotope of sodium, Na-24.'[893] This was still news and sodium-24, as a Penguin Special on *Atomic Energy* (1950) explained to the enlightened public, belonged to those isotopes 'regularly produced' and 'in frequent use' in biology and industry. 'It's half-life is 14.8 hours, and a beta particle of maximum energy 1.4 MeV is emitted in cascade with 2 gamma rays of 1.38 and 2.76 MeV energy. The sodium is, therefore, extremely easy to detect'.[894]

Such were 'the constructive uses of atomic energy'.[895] And they were, at times, extremely easy to detect - by electronic means. Injected into rabbits or rats, or red blood cells washed in radioactive saline solutions, Na-24 penetrated biological systems; the muscles of young rats unquestionably accumulated sodium (when kept on a potassium-deficient diet for several weeks).[896] And in red blood cells, it had dawned by 1941, it mixed with the intracellular sodium, ions *exchanging* as Geiger counters clicked away: 'In 18, 26, and 64 minutes the cell counts were represented by 126, 175, and 219 respectively showing a gradual penetration of Na-24.'[897]

Richard Keynes, transplanted back to Cambridge from the Admiralty Signals Establishment, Surrey, by 1946 was also busy adapting radioactive tracer techniques to

[892] See Hodgkin, typescript, Cold Spring Harbor Talk (1952), p.3 , HDGKN E.6
[893] Fenn (1949): p.20.
[894] Crammer and Peierls (eds.) (1950): pp.128-130.
[895] Crammer and Peierls (eds.) (1950).
[896] E.g. Heppel (1940); E.J. Conway and Hingerty (1948).
[897] Manery and Bale (1941): p.228.

chart the movements of ions through the active nerve membrane . The hope was, of course, to penetrate the elusive ionic dynamics behind the puzzling *reversal*.[898] Keynes, whose war-time patent track-record included such items as 'multicolour [radar] displays' - 'polychromatic … presentation' of 'information' - had few difficulties, we must assume, when it came to coaxing a Geiger-counter into operation.[899] By 1947, he first supplied suggestive evidence along these lines for a 'net leakage' of potassium during nervous activity, results obtained with *Sepia* axons soaked in a radioactive potassium. The 'rate of loss' roughly tripled under rapid stimulation – here the former *potency* of ionic agents turned into *rates*.[900]

Such 'net leakage' became manifest as an accumulative effect – after hundreds of stimuli: a question of *minutes*. It now became manifest, however, amidst an ever-expanding world of ionic fluxes, rates and surface processes. By now, Hodgkin's interest in sodium had indeed made a considerable leap. '[E]xchange of external Na with internal K', Hodgkin pondered in October 1946, might be 'essential for propagation [of the impulse].'[901] It was a big step for the action potential problem, but only a small step to make in this world; in fact, it was courtesy of a very *low-tech* means they had devised to probe something far less outlandish: the time-course of potassium *leakage*.

Making their way into a short note published in September 1946 in *Nature,* Hodgkin and Huxley's come-back experiments had centred on a peculiar oil-immersion technique: rather than simply bathing the axon in sea-water, they first immersed it in paraffin oil. The purpose: to reduce the volume of the external electrolytic solution to a thin film surrounding the axon. The result: a hopefully clearer picture of the 'time course' of the minuscule potassium leakage from an active nerve.

The accumulating potassium, now readily apparent relative to the thin film of sea-

898 Morison, Interview with Hodgkin, July 8 1949, copy in RF/RG.1.2, 401 A, Box 13, F older 114
899 See application drafts (1945) by Keynes, ADM 1/15239; and 'Multicolour Displays' (April 1946), ADM 220/89
900 Keynes (1948).
901 Hodgkin to Cole, 17 October 1946, HDGKN D.96

water, 'prov[ed]', what Keynes soon confirmed by way of radioactive tracers, namely, 'that [nervous] activity was associated with the leakage of a substance the effect of which on the nerve membrane is very like that of potassium.'[902]

There was no public mention of a sodium hypothesis, not even, sodium. Behind the scenes, however, sodium evidently had caught the attention of the nerve-team. This was because, curiously indeed, in these leakage experiments one had observed potassium being *re-absorbed* by the axon – *against* the ionic concentration gradient. As one of the 'many things which cannot be put in scientific papers', Hodgkin, in turn, had begun to ponder an 'active extrusion of sodium': It would be the 'most likely type of mechanism' to keep the ionic balance – with the corresponding amount of potassium ions entering through 'exchange'. There was 'no real evidence' for such extrusion.[903] But certainly, extrusion implied prior entrance.

Seeing such sodium-extrusion, unlike in 1939, or even in 1945, was no longer magic. A mass of data pertaining to the 'ionic composition' of sea-water, tissues generally, and the axoplasm of the squid giant axon in particular had long begun to pour in (thanks, not least, to its convenient giant size). At Woods Hole alone 'the queue [working on the squid giant axon] now makes to 12-15 scientists!' as Hodgkin approvingly recorded by 1948.[904] Already in 1943, significantly revised estimates for the sodium-contents of these axons had been obtained by the zoologist Burr Steinbach, one of the scientists queuing at Woods Hole.[905] All this brought the sodium *imbalance* into a range where sodium much more plausibly would have appeared as the possible missing agent with regard to the action potential. In this world it was no longer inconceivable that sodium ions *entered* the cell, and fairly quickly at that.

The spell was broken: Katz, joining Hodgkin's team in the fall of 1946 at Plymouth,

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902 Hodgkin and A.F. Huxley (1946).
903 Hodgkin to Cole, nd (c.1947), HDGKN H.24
904 Hodgkin to Young, 20 April 1948, YOUNG, 93/89
905 Steinbach and Spiegelman (1943): pp.187-189.

promptly entangled sodium and the impulse even more intimately - by adopting the oil-immersion technique above. Once so immersed, successive reductions of the 'salinity' of the immersing electrolyte-fluid had a 'pronounced' effect, Katz showed, on the speed and shape of the impulse. In the limit: no sodium, no conduction. Without the oil-bath, the consequences were barely perceptible.[906]

When his results went to the press in the early 1947, Katz did not even gesture towards an hypothesis.[907] Privately, however, the nerve-team was groping for a *picture*. The 'whole thing is highly speculative', Hodgkin warned Cole. There already had been forming in his mind a picture of the action potential problem that would critically involve: sodium.[908] It made the team venture into utterly speculative, unknown territory: these pictures operated at the fundamental level of membrane molecular processes. Hodgkin envisioned, for instance, that the action potential might be the 'direct result' of certain ionisation processes at the membrane. External calcium ions, assumed to stabilize the resting membrane, would be suddenly removed, de-stabilize the membrane and allow extra-cellular sodium to enter through the membrane, possibly via some intermediate 'carrier' molecule: a sudden ionic inrush - a *current* carried by sodium - would be the result, *hyper-polariz*e the cell surface (relative to the resting potential), and so account for the 'overshoot' - the mismatch between resting and action potential.

And here it was, in essence, the solution to the action potential problem: the sodium hypothesis; but not its form. Speculation was something quite intolerable for these practical physicists, or electro-engineers of nerve; their picture, accordingly, was to be a definite one. It was difficult to see, as Hodgkin said, how any such complex scheme could 'work out quantitatively'. And worse, there was a 'real difficulty to know how to apply experimental tests'.[909]

[906] Katz (1947).
[907] Ibid., esp. p. 412 .
[908] Hodgkin to Cole, 17 October 1946, HDGKN D.96
[909] Ibid.

Defining the impulse

> *'[Y]ou will remember, the brain tends to compute by organizing all of its input into certain general patterns. It is natural for us, therefore, to try to make these grand abstractions, to seek one formula, one model, one God, around which we can organize all our communication and the whole business of living.'*[910]

The series of 'test solutions' prepared at Plymouth during the summer and fall of 1947 systematically *varied* this one specific factor: 0.0, 0.2, 0.33, 0.50, 0.715, 1.26, 1.56 - sodium concentration expressed as fractions of seawater; effects on the impulse recorded. A kind of variational method. The result: masses of data, figures and curves; not quite yet a *definite* picture, let alone 'one formula'.[911]

But there was a mission now. In *developing* their sodium 'effect' into a model of nerve behaviour, the still rather vague notion of inrushing sodium had pointed the way forward. In the hands of the Cambridge nerve-team the putative inwards movements of these newly palpable sodium ions now turned successively into a hypothesis, a 'coherent picture', a quantitative formulation, a 'general' sodium *theory* - and eventually, into the core of their full-blown 'reconstruction' of a nerve's electrical behaviour.[912] In the process, ions were moulded into 'component currents'; measured, quantified and theorized, they were ever more deeply knitted into the fabric of the world of electronic scrap, electronic assistants, and borderland scientists. Successively, as we shall see in the remainders of this chapter, the elements and layers of this newly resolved world - quantitative formulations, squid, theoretical membranes (circuits), oscilloscope curves, electronic design, and numerical practices - were assembled into a *definite* picture of the cell's bioelectrical

[910] Quoted are Young's BBC Reith lectures, published as J.Z. Young (1951): p.163.
[911] The resulting paper was not published until early 1949, see Hodgkin and Katz (1949): p.49.
[912] See Hodgkin and Katz (1949); Hodgkin (1951); Hodgkin and A.F. Huxley (1952a).

behaviours.

The emergent, ionic vision of the nerve impulse would not be a micro-physical, ‘speculative’, molecular scheme of membrane processes. Hodgkin and his team-mates quickly relinquished this ideal of ultimate *representation*. In its place came a ‘theoretical reconstruction’ - but one tightly enmeshed with the material world. In this model cell, I shall argue, describing, producing and computing the phenomena merged into virtually one, singular activity. And nothing in this process will particularly surprise us: they had acquired, after all, the ‘frame of mind’ of the practical rather than theoretical physicists – ex-radar personnel.

By squid season 1947, the joint Cambridge-London programme was thus making significant inroads into the sodium effect - by means of advanced circuitry: ‘electrical differentiation’. Implemented by plugging a ‘condenser coupling’ into their amplifier set-up, such circuit-wizardry allowed the team to directly measure the *rates* of the potential change rather than, as would have been customary, the magnitude of the potentials. The peculiar type of record this yielded only appears familiar. These curves revealed *speeds* - as a *function* of extra-cellular sodium concentrations: a more or less rapid rise of the potential in its initial stages, followed by a sharp decline; the more sodium in the surrounding fluid, the sharper the onset of potential surge. To the tuned eye, they revealed ionic dynamics.[913]

[913] Hodgkin and Katz (1949): p.40.

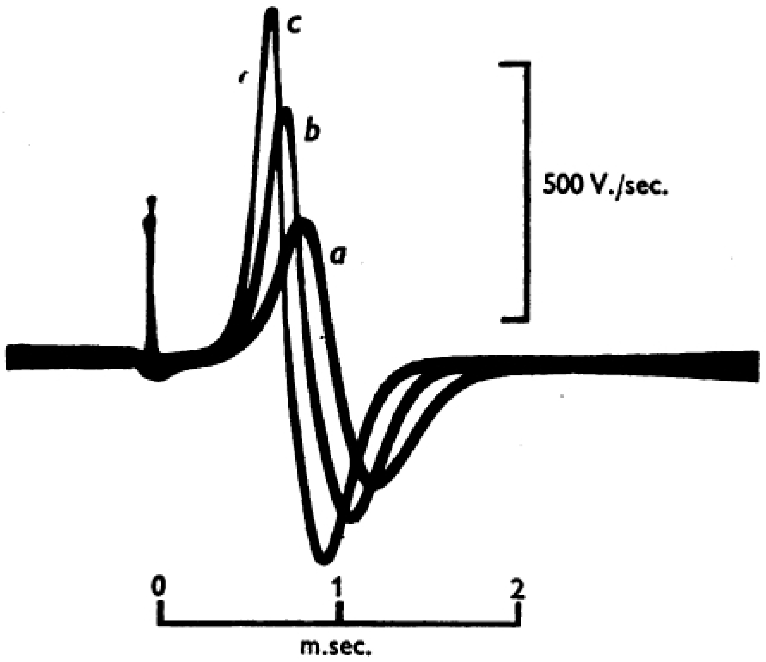

Figure 53: Rates of potential change as a function of external sodium concentration, 1948

This was the sodium *hypothesis,* almost plainly visible. The sharp onset: a sudden, inward-directed sodium current; the decline: 'deactivation' of the sodium current accompanied by a delayed outflux of potassium; finally, return to resting conditions.[914]

By way of electrical differentiation the once compact entity of the action current had begun to decompose, definitely. The concrete picture of impulse that began to take shape was not longer that of an atomic unit but rather that of a composite, temporal structure. This evidently was not a digital signal. This was very analogue indeed: a superimposition of multiple ionic currents each with its specific and individual dynamics. The same, coarse picture was easily reproduced once Keynes got hold of sodium-24 around at the same time; the sodium 'net entry', Keynes showed, increased some seventeen-fold in the active nerve.[915]

'Your sodium story', Cole wrote in early 1948, 'is certainly very thrilling'.[916] The paper that had made public that summer's result, worked out by Katz and Hodgkin during

[914] Ibid., pp. 57-58.
[915] Keynes (1949).
[916] Cole to Hodgkin, 26 April 1948, HDGKN H.10

the winter of 1947/48, had confidently set forth this story, or an 'hypothesis' in their words, of the 'simpler type': it posited that the 'active membrane' didn't merely lose its selective permeability but instead 'revers[ed] the resting conditions by becoming highly and specifically permeable to sodium.'[917]

All other explanatory scenarios for the 'reversal' that had been cropping up of late they dismissed as hopelessly 'speculative'. They cavalierly rejected the proposition, for instance, by the ageing Höber, of enrolling 'nonpolar-polar, hydrophobic-hydrophilic anions' into the picture, which presumably existed dormantly (waiting to be 'liberated') especially in certain 'phospholipid', 'cerebroside' and 'oxynervonic' membrane-molecules of the nervous system.[918] These Cambridge men reasoned in electrical quantities, not in molecules. Expressed, roughly, in terms of membrane 'charge', the situation presented itself thus: empirical values for the resting conditions amounted to some 90 mμ coulomb, and to about 60 mμ coulomb for the 'reversed' charge of the active membrane. In total, some 150 mμ coulomb evidently had to be 'transferred' in the process, a figure corresponding - in theory – to some 1.6 μμ mol of sodium ions entering the nerve.[919]

The question was how. But here was palpable a *pattern*: the nerve-team now operated and observed amidst an abundance of data pertaining to the ionic composition of the world.[920] Whether in the squid giant axon ('material ... most suitable for permeability studies') or other 'simple cell models' such as erythrocyte 'ghosts', frog skin, and artificial 'permselective' membranes observations on 'biological transport' were plentiful, and quantitative.[921] Katz and Hodgkin promptly bolstered their interpretation with a 'quantitative formulation' of the hypothesis: a 'simple equation'; 'no more than a rough

917 Hodgkin and Katz (1949): pp.37-38; and p.55.
918 Höber (1946): p.388; Hodgkin and Katz (1949).
919 The figures are based on Hodgkin (1951).
920 To get a sense of the impetus permeability investigations in particular received from tracer methods, see e.g.Teorell (1949b); Steinbach (1951).
921 Cited are Rothenberg (1950): p.96; Teorell (1952): p.669.

approximation', they repeatedly emphasised. The 'object' was 'to show that a large number of observations can be fitted into a 'coherent picture'.[922]

These large numbers readily collapsed into such a coherent picture when one assumed, as did Hodgkin and Katz, that the membrane potential difference was essentially determined by only three, individual ionic components – sodium, potassium and chloride – and second, that ionic movement across the membrane was primarily determined by only two *physical* factors: diffusion and the electrical field set up by the potential difference.

Further *definition*: it was possible to relate ionic 'permeabilities' (the individual membrane-currents) and the potential difference by way of the following, fairly standard diffusion equation:

$$E = \frac{RT}{F} \log_e \left[\frac{P_K (K)_i + P_{Na} (Na)_i + P_{Cl} (Cl)_o}{P_K (K)_o + P_{Na} (Na)_o + P_{Cl} (Cl)_i} \right]$$

There were no secrets involved, only some 'radical simplifications' (for instance, the whole scheme evidently made now allowance for 'active', metabolic reactions). In the above equation, originally derived in similar form, if only for different purposes (and without consideration of sodium), by a PhD student of Cole's, David Goldman, the respective permeabilities - with values 'found' by 'trial and error - entered as P_K, P_{Na}, and P_{Cl}.[923] Goldman had been chasing non-linear potential-current relationships, not the specifics of ion dynamics; in Cambridge, one chased the latter: their adapted equation accurately 'fitted' the observed potential curves when the sodium permeability underwent a twenty-fold increase; or more specifically, when the ratio $P_K : P_{Na} : P_{Cl}$ was shifted from 1 : 0.04 : 0.45 (resting potential) to 1 : 20 : 0.45 (action potential).[924]

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[922] Hodgkin and Katz (1949): pp.66-67.
[923] Hodgkin and Katz (1949): p.66; and see Goldman (1943).
[924] Hodgkin and Katz (1949): p.68.

This was a 'picture', not a 'reconstruction'. But even so, it was an almost instant success. Qualitatively, the hypothesis was easily grasped, and its formal and experimental execution impressive. 'Nice stuff', as Ralph Gerard wrote.[925] Within a short period of time, the becoming manifest of sodium had re-framed the puzzles surrounding nervous activity. Whether one embraced it (and many did) or not (as some did), the hypothesis was the force to be reckoned with: a topic of 'repeated discussions'.[926] Not, evidently, that there was a shortage of alternatives - speculations, explanatory scenarios and possible 'special mechanisms'. Rosenblueth and Wiener's intricate mathematical forays into non-linearizing the axon were just about to see public light (drawing for these purposes on data published, notably, by Hodgkin and Huxley).[927] Kenneth Cole, too, was still, or again, pursuing a non-linear membrane element. His quest had been fuelled additionally by investigations on suspiciously analogue, 'rhythmic reactions' of a wire immersed in acid by Max Delbrück's brother-in-law, the physical chemist Karl Friedrich Bonhoeffer and his *Arbeitskreis*.[928]

Especially Cole was 'very enthusiastic' about this *Modellversuch* it was reported back to Germany, Delbrück 'slap[ping]' on himself and his CalTech students the 'requisite mathematics (non-linear differential equations)' as well.[929] Ultimately, however, to little avail. The sodium effect didn't mesh very well with such scenarios and no longer did inanimate objects like wires enjoy unanimous epistemic respect.[930] This was one appalling exemplar of 'useless analogy', as Wiener and Rosenblueth's essay 'The Role of Models in Science' summed up the new mood: 'The phenomena of passive metals are not better understood than those of nerve'.[931]

925 Gerard to Hodgkin, 11 October 1949, HDGKN H.18; Monnier to Hodgkin, 27 April 1948, HDGKN H.10; Grundfest to Hodgkin, 21 March 1949, HDGKN H.19
926 Mazia to Hodgkin, 30 July 1951, HDGKN H.20
927 Wiener and Rosenblueth (1946); Rosenblueth, Walter Pitts, Ramos, and Wiener (1948).
928 See correspondence with Delbrück, BONHOEFFER
929 Letters Delbrück to Bonhoeffer, 28 December 1947; Delbrück to Bonhoeffer, 12 November 1952, BONHOEFFER
930 Miles (1972).
931 Rosenblueth and Wiener (1945): p.318.

But let us not follow too quickly on the epistemic heels of those dismissing these humble objects from their role in science. Like the less noble, but extensive work on frog skins, red blood cell 'ghosts', artificial membranes, and such technical matters as electrophoresis which surrounded the biophysics of nerve and did much, in fact, to make more transparent the world of ionic transport, this wire was an object being *worked* with. And it was quite capable of producing significant, *real* model-effects, as we shall see shortly.[932]

Neither let us be too distracted by the appearance of the circulating *products*: equations appearing in print. This is not how (even formal) models exist, or what makes them *real*. Coherence, definition, and communicability was one thing; it was – now - also the work that went into producing equations, or coherent pictures, the labour of computing them, and, not least, making them 'conform' with the phenomena. Or this, at any rate, will bestow on the model that issued from the hands of Hodgkin, Huxley and Katz the unique import and reality effects it had in the post-war world. There was neither the convoluted, vague empiricism of the biochemists, nor the merely abstract struggles of a Wiener.

We are now in a good position to see how this model-cell was not due to genius, but an articulation of the cell's mundane, electronic life-world. In Cambridge, these things merely came together in concentrated fashion. There, work on a definite picture still had hardly begun. Making the 'coherent picture' into a 'theoretical reconstruction', as we shall now see, meant re-designing the phenomena themselves, quite literally.

[932] For some important intermediaries between these various domains, see Ussing (1949); Teorell (1949a); Sollner (1950); Sollner (1953); E.J. Harris (1960); also see Chiang (2008).

Re-engineering the impulse

'Abstraction consists in replacing the part of the universe under consideration by a model of similar but simpler structure.'[933]

Cambridge was turning, as team-leader Hodgkin approvingly observed in 1950, into 'an active centre of what is now known as Biophysics'.[934] New on board were such figures as William Nastuk, Robert Staempfli, or Silvio Weidmann: 'Experimental work', as Weidmann had advertised himself, 'may be facilitated by the fact that I am relatively familiar with electronics.'[935]

Here definition in the picture corresponded to definition in practice; a great deal of work thus went into refining and expanding the numerical picture of the action potential. From a visit to Chicago in 1948, Hodgkin had imported 'true' micro-electrodes, a recent innovation courtesy of Gerard's laboratories where one specialized on the much less glamorous *resting* potentials of muscle cells.[936] The Cambridge-team, in turn, 'recogniz[ing] a good thing when [they] saw it', lost no time in extending their own programme beyond the giant axon to a much broader and persuasive assortment of (single) nerve, heart and muscle cells - their former owners ranged from squid, sepia, and crab to vertebrates such as frogs and dogs.[937]

In what was an empirical tour de force, Hodgkin presented the much improved case to the world in 1951, confidently turning the sodium story into a 'general hypothesis'. This 'picture of the sequence of events during the nervous impulse' came dispersed over some seventy pages, in words, tables, curves, and an infinite amount of data on ionic tissue concentrations, ionic exchange rates, and electrical properties:[938] a general, but disturbingly empirical and disconnected picture. The nerve-team, too, was haunted by what was an

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933 Rosenblueth and Wiener (1945): p.316.

934 See 'Biophysical Research in the University of Cambridge' (October 1950); and Application to Nuffield Foundation (October 1950), in HDGKN B.5

935 Weidmann to Hodgkin, 27 March 1948, HDGKN H.30

936 Hodgkin (1950): p.322; Squire (1996): p.186.

937 Hodgkin to Ling, 10 August 1949, HDGKN H.18

938 Hodgkin (1951): esp. pp.339-340.

increasingly complex situation after all, and thus, difficulties of description, coherence, and communicability. Worse, as Cole later reminisced, the nerve membrane was on the whole a 'disgustingly unstable device'.[939] As for Cole, Wiener and Rosenblueth, as well as for a number of others who had begun to despair over the vexing non-linearities of nervous behaviour (and had resolved for themselves that the computational labour involved in a 'complete theory of conduction' would be 'considerable unless a machine is used'), in Cambridge these issues had become more, rather than less, virulent.[940]

The major problem with their hypothesis, as the Cambridge team saw it, was indeed that it wasn't even remotely evident what kind of physical mechanism would underlie their picture: a sudden and *specific* increase of a membrane's permeability to sodium ions – or the equally sudden, subsequent reversal of this condition: its 'exhaustion or inactivation'.[941] The membrane might well be envisioned to contain certain lipoid-soluble 'carrier compounds', as Hodgkin confessed his growing qualms at a gathering of the so-called Hardy Club in 1950, a local gathering of biophysicists that prominently included such ex-radar folk as Hodgkin, Huxley, Keynes, Pringle, Crick, and Kendrew. But these compounds were a most hypothetical construct, backed by no empirical evidence whatsoever: 'a lot of speculation'. Worse: 'even if you accept the existence of such carriers', Hodgkin cautioned, 'you still have to explain why it is that these carriers are only able to carry Na or K when the membrane is depolarized.'[942]

The microcosm of the cell, despite the electron-microscope, despite the nascent molecular biology, and despite all the biophysical furore remained, for the time being, a space unimaginable in any secure detail. As far as 'definite' pictures were concerned, micro-physical mechanisms had been shelved. Their place was taken by measurable, *definite* and computable entities: ionic fluxes, thoroughly defined rather than speculatively imagined.

[939] Cole (1975): p.148.
[940] See esp. Offner, Weinberg, and G. Young (1940).
[941] Hodgkin and Katz (1949): p.38;p.70.
[942] MS for Hardy Club lecture (1950), p.9, HDGKN E.4 ; on the Hardy Club, see Chadarevian (2002): p.91.

Such a 'model satisfies', as Pringle had it, 'if the mathematical formulation of its performance is identical with that of the original system.'[943]

Performance is a term to be taken seriously here. As the following shows, the reality effects this model-cell produced owed much to its concrete (rather than merely mathematical) performativity, and little to any representational function. Its relations to the world were intimate and multiple. That was the trajectory things had already been taking in Cambridge. And by the time of Hodgkin's Chicago stint in 1948, further steps towards an eventual resolution had already been underway. It was a true piece of electronic bioengineering.

The original purpose of Hodgkin's trip to Chicago had not been true micro-electrodes, but a visit to Cole's new home, the (also new) Institute for Biophysics and Radiobiology. And although we cannot be certain, this is what we must imagine Cole and Hodgkin discussed as they strolled over the progressive Chicago campus:[944] to model the impulse, it first had to be eliminated – literally.

Barring convoluted, verbal and qualitative pictures as complex and incommunicable as the phenomena themselves, the straightforward, but equally unsatisfactory solution to their complexity-problem was to reduce the complexity of the description; to simplify, in other words, the mathematical formulation: less detail, fewer parameters, less labour, less identity in performance with the original system: The impulse, that was, naturally pictured as a travelling wave. The alternative was to reduce the complexity of the phenomena themselves: prior to modeling them.

Here was 'the hottest thing' in post-war physiology.[945] Wiener's philosophical sneers

[943] Pringle (1960): p.42.
[944] Cole, 'Genesis of the Voltage Clamp: A position Paper', October 1963, OSTERHOUT, Box 1, Folder 'Cole'; Miles (1972); A.F. Huxley (1992): p.30; on Chicago, see Rheinberger (2001): p.152; Reisch (2005): p.39 and passim.
[945] In the words of ex-radar biologist Seymour Benzer. See Aspaturian (1990): p.15.

notwithstanding, it involved a little, practical side-role for passive metals. The basic idea was simple enough. To analyse the active membrane in as precise a manner as possible, it various components would have to be *controlled*. Getting rid of its capacitive component, for instance, would leave only the current due to ionic displacements. And getting rid of a further variable that complicated analysis - movement in space - meant to eliminate the disturbing propagation of the impulse itself. The impulse would be electronically *dissected* - controlled, stalled in space, and simplified: something amenable to rigorous analysis.

Whether or not Hodgkin already arrived in the US with these things in mind (as Huxley remembered) is quite immaterial to the present story;[946] the means, electronic feedback control, was hardly news to an ex-radar man; and at any rate, as Grey Walter wrote in his *The Living Brain* (1953), in the form of goal-seeking missiles for instance, they were 'literally much in the air in those days; so in our minds'.[947]

What is certain, however, is that Cole had long been pondering methods of 'potential control'.[948] Cole's own mind had been stirred, quite concretely, by the Chicago physicist James Bartlett. Like Bonhoeffer's *Arbeitskreis*, Bartlett had became interested in the 'parallelism' between 'transients' in nerve cells and the ones occurring in those intensely investigated systems he knew about most: passive metallic systems – anodic phenomena. The serious study - and production - of these latter phenomena necessitated, Bartlett found, the application of 'sudden' voltage shifts so as to keep the system in a stable - and analysable - state.[949] By 1948, Bartlett had proposed a 'thorough' analysis of these analogous 'circumstances' in the *Journal of Cellular and Comparative Physiology*; and by then, definite steps towards transferring the control-concept to real nerve had been made as well.

Cole's new assistant, the Caltech trained biophysicist George Marmont, clearly

[946] A.F. Huxley (1992): p.30.
[947] Walter (1953a): p.82.
[948] Bartlett (1986).
[949] See Bartlett (1945); Bartlett (1948).

knew how to manipulate circuitry. Marmont had spent the war at the Bendix Aviation Corporation, Detroit, and several patents on electronic gadgets - ignition systems (and less martial, an 'electronic musical instrument') - already carried his name when in the course of 1946 he began to devise means to eliminate the nerve impulse.[950]

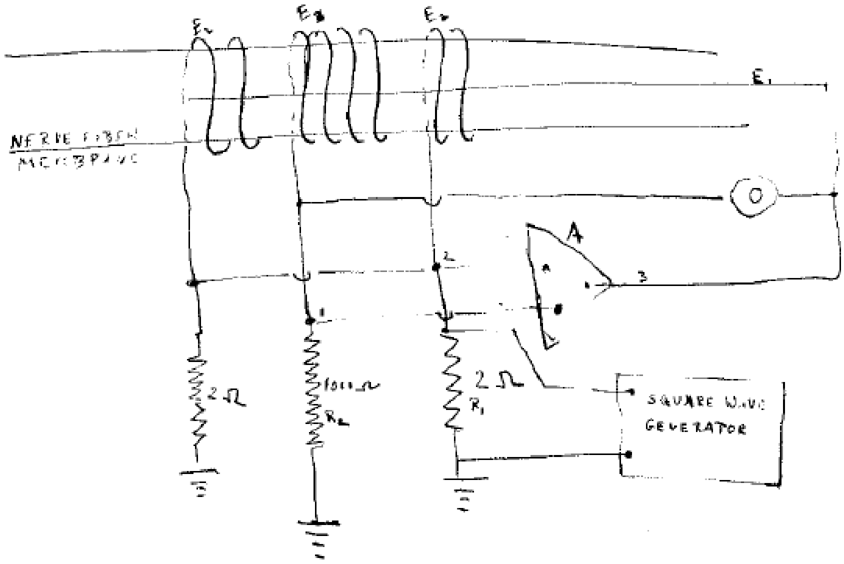


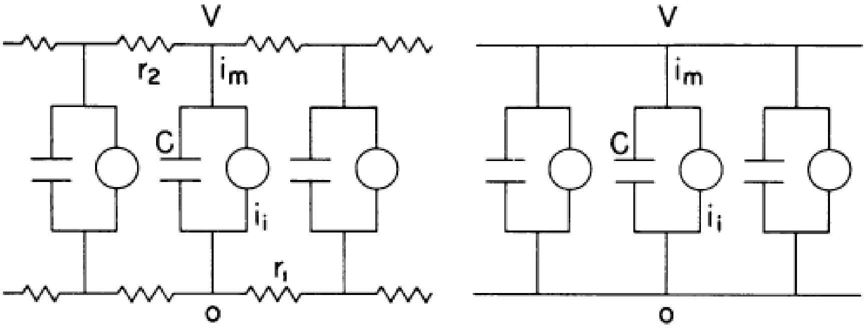
Figure 54: 'Marmont's set-up', sketch by Max Delbrück, 1947

'Here electronics enter[ed] the picture', as Marmont announced.[951] And already by 1947, it had been making its rounds - via Max Delbrück and as a circuit-diagram – for instance, to Germany.[952]

'What one would really like to do', Marmont explained, was to 'be able to control the current density or the potential drop across the membrane or some other parameter ... regardless of whether the membrane became active or not.' This meant, in plastic terms, that the 'effects of propagation will be removed from the experiment'.[953] Parameters such as distance, velocity, excitation threshold, or the all-or-none behaviour of nerve then simply vanished, simplifying the phenomenon and the analysis as well. Even visually: circuit a)

[950] Miles (1972); Marmont (1949b/1946).
[951] Marmont (1949a): p.353.
[952] Delbrück to Bonhoeffer, 16 October 1947, BONHOEFFER
[953] Marmont (1949a): pp.351-352.

under such ‘circumstances’ transformed into the much simpler circuit b).[954]

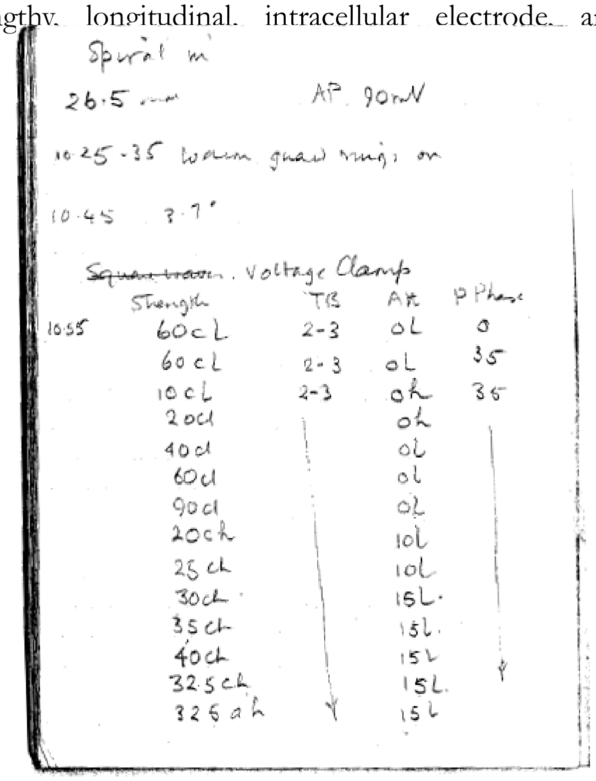


$$a)\ i_m = C\frac{\partial V}{\partial t} + i_i = \frac{1}{r_1 + r_2} \cdot \frac{\partial^2 V}{\partial x^2} \qquad b)\ i_m = C\frac{dV}{dt} + i_i$$

Figure 55: Re-engineering the ‘situation’.

It was clearly an ‘ingenious’, ‘complicated’ arrangement, as *Scientific American* reported in 1949.[955] Feedback-control transformed the axon-electrode system into a stretch of uniform, controlled membrane conditions. Technically, this re-engineering feat was achieved by inserting into the system an ‘electronic feedback circuit’; a squid axon, a lengthy, longitudinal, intracellular electrode, and three external ‘guard’ electrodes complemented the system.

This techno-organic gadget would make feasible a ‘definite picture’ of the action potential. But, the picture would be of British vintage. Cole and Marmont’s paths diverged as Cole moved on, in 1949, to the Naval Medical Research Institute in Bethesda, Cole being considerably distracted henceforth with


Spiral m
26.5 mm AP 90mV
10.25-35 warm guard rings on
10.45 7.7°
~~Square wave~~. Voltage Clamp

	Strength	TB	Att	P Phase
10.55	60cL	2-3	oL	0
	60cL	2-3	oL	35
	10cL	2-3	oL	35
	20cl		oL	
	40cl		oL	
	60cl		oL	
	90cl		oL	
	20ch		10L	
	25ch		10L	
	30ch		15L	
	35ch		15L	
	40ch		15L	
	32.5ch		15L	
	32.5ah		15L	

Figure 56: Voltage clamping, 1949 (page from Hodgkin's Notebook)

[954] Cole (1962): p.111.
[955] Pfeiffer (1949): p.16.

questions of 'preparedness'.[956] Back in England, by the squid season of 1949, Hodgkin, Huxley and Katz had their own system running. Notebooks gradually filled up with masses of ever improved 'voltage clamp' records, as they patiently coaxed their unstable, bioelectronic device into operation: heaps of data gathered, curves, photographs and tracings piling up. Such was, after all, the nature of even 'pure research with a complicated apparatus' as W.B. Lewis, one of Hodgkin's TRE superiors, had pondered his recent experience in microwave radar:

> Before [a] phenomenon can be observed as a matter of routine by even a trained operator, it is necessary to carry out applied research into the properties and limitations of the refractory components and, as a result, to redesign or "engineer" them to perform their function with certainty.[957]

Describing = Intervening = Computing

From 1949, impulses did no longer propagate in Cambridge. At the same time, the British usage of the 'feed back' technique differed subtly, but significantly, from the ultimately far less productive one which Cole and Marmont had adopted. The latter had opted for a mode of operation that made perfect sense to the vision of nerve Cole had been developing. This centred, we will remember, on the electrical, presumably non-linear properties of the membrane. For these purposes - to get an unspoilt view on the electrical conditions of the membrane - it was desirable to keep the net current flow through the membrane uniformly at zero, even during a 'response'.[958]

It was ionic currents, in other words, that were eliminated as a variable. This made far less sense if one was interested, as was the Cambridge nerve-team, in dissecting these very currents: they, accordingly, eliminated potentials.[959] Producing a controlled, uniform potential, and 'suddenly' displacing it 'in a stepwise manner' to a different level would

956 Miles (1972).
957 W.B. Lewis, The Role of T.R.E. in the National Scientific Effort (1945), AVIA 15/2260
958 Marmont (1949a): p.356.
959 Hodgkin, A.F. Huxley, and Katz (1952): p.446.

effectively reproduce, as they argued, the conditions of an impulse, only simpler. 'Under these conditions', Hodgkin, Katz and Huxley will phrase it, the sudden displacement of the potential induced an equally sudden 'surge' of capacity current, followed by an ionic current; the potential, meanwhile, was simply maintained – by way of feedback control - at a different level.[960]

Having redesigned the refractory component of the system, the different ionic component currents could be precisely taken apart – *functions* of the detailed manner the potential was displaced: an initial, transient sodium current, its inactivation, a delayed potassium current. This was the 'picture of the sequence of events' - given concrete, controlled definition. The membrane current had been 'resolved', as they wrote in 1952, into its several components. [961]

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In between were spaced three squid seasons of patient engineering and re-engineering, and three winters of exploring on paper and Brunsviga calculation machines 'definitions', 'subsidiary equations', and the agreements of data and computations: 'permeability' changes, ion 'flux', 'conductance' and more. Eventually, some twenty empirical constants had to be defined, measured and entered into the complicated equations the team had begun to develop. This was the labour of many months, a patiently constructed model, albeit not from 'first principles' (as they emphasized).[962]

The famous series of five papers in 1952 constructed the definite picture step-by-step, culminating in the detailed 'reconstruction' of nerve behaviour. It was amazingly accurate, but one might well be 'appalled ... by the formidable empiricism of the formulation', as Cole reaction was in 1952. Clearly, this wasn't a 'theory of the underlying mechanisms'.[963]

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[960] Ibid., esp. p.425.
[961] Hodgkin and A.F. Huxley (1952b): p.471.
[962] Hodgkin and A.F. Huxley (1952a): esp. p.506; nn. (1952a): pp.51-52.
[963] nn. (1952a): p.51.

Little survives of this intermittent phase of data production, processing and modeling, and the point here certainly is not to provide a detailed technical micro-history of the model's genesis. In fact, not much would follow from such an exercise. There was no mystery. Hodgkin and his team of ex-radar biologists did what they had learned: they produced a controlled laboratory effect and simultaneously devised its numerical 'picture'. Or rather, they designed a system that would exhibit 'identity in performance'.

What deserves emphasis are the intimate relations between electronics, numerical practice, and the phenomena themselves that were being forged in the process. It is both what set this model-cell apart, and what made it *real*, deeply woven into the material fabric of this more intensely quantified, traceable world.

Although temporally spaced apart, modeling and intervening, predicting the bioelectrical effects, shapes, and wave patterns one designed, were activities tightly intermeshed, not separate enterprises. Definition was integral to intervening, and computing to describing: The entire 'design and analysis' of these experiments, as they said, necessarily operated on the basis of certain theoretical assumptions.[964] No patterns would be discernible without the construct of a 'theoretical membrane'. At every step, practice, modeling, and manoeuvres of simplification had been entangled. Even the most basic manoeuvre, potential control, was so given its rationale:

In first approximation, the membrane current could be conceived of as the composition of a capacity current (due to the membrane capacity) and the sum of the several ionic currents composing it; or, in formal language, this state of affairs was described by the differential equation:

$$I = C_M \frac{\partial V}{\partial t} + I_i,$$

[964] Hodgkin, A.F. Huxley, and Katz (1952): p.425.

Clamping the potential at a constant level (in which case: $\partial V / \partial t = 0$) reduced the first term to zero, so that only the ionic current remained. This current could then be 'obtained directly' by way of measurement. And this was, the nerve-team explained, 'the most obvious reason for using electronic feed-back to keep the membrane potential constant.'[965]

Around this basic manoeuvre, equations designed and defined 'to make them fit the phenomena' - and vice versa – phenomena designed to fit the equations - coalesced into a quantitative 'model'.[966] The second paper of the series thus would at length discuss the definition of ionic 'conductance' as a measure of the all-important membrane permeability.[967] The next instalment, meanwhile, dealt with the detailed time course of the various ionic components, and in particular, the sudden, transient inrush of sodium and its equally sudden 'inactivation'. The fourth, in turn, treated the degree of (non-linear) dependency of such 'conductance' on the membrane potential.[968] Putting it all together yielded a set of differential equations: they described the membrane current as a function of time and potential, and second, the temporal trajectory of three factors - ominously labelled *n*, *m*, and *h*.[969]

965 Ibid., p.452.
966 Hodgkin and A.F. Huxley (1952a): p.541.
967 Hodgkin and A.F. Huxley (1952b).
968 Hodgkin and A.F. Huxley (1952c); Hodgkin and A.F. Huxley (1952d).
969 Hodgkin and A.F. Huxley (1952a): p.518.

$$I = C_M \frac{\mathrm{d}V}{\mathrm{d}t} + \bar{g}_K n^4 (V - V_K) + \bar{g}_{Na} m^3 h (V - V_{Na}) + \bar{g}_l (V - V_l),$$

$$\mathrm{d}n/\mathrm{d}t = \alpha_n (1 - n) - \beta_n n,$$

$$\mathrm{d}m/\mathrm{d}t = \alpha_m (1 - m) - \beta_m m,$$

$$\mathrm{d}h/\mathrm{d}t = \alpha_h (1 - h) - \beta_h h,$$

This was the reconstruction - on paper. When fed with data, constants, and implemented on calculation machines it *performed* identically. 'An equally satisfactory description' of the electrical behaviour of the membrane, as Hodgkin said, 'could no doubt have been achieved with equations of very different form'.[970] Notably the factors *n,m,* and *h*, thus were almost wholly arbitrary, 'dimensionless variables'.[971] As to performance, however, they were crucial. They reproduced the variation with time of the three ionic conductances: sodium, potassium, and a 'leak' component. The time-course of sodium permeability, for instance, could be described by an equation of the form:[972]

$$g_{Na} = m^3 h \bar{g}_{Na}$$

Nothing here pointed to, or *represented,* any particular 'mechanism of permeability change' in particular. What the model did was to suggest a definite picture of the sequence of events.

And it was computability that dictated the shape the picture assumed. These equations weren't merely 'empirical'. They were computable - practically solvable. To make the description *perform*, complex equations had to be reduced to appropriate forms. A

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970 Ibid., p.541.
971 Ibid., p.502; p.504; p.507; pp. 540-541.
972 Ibid., p.512.

routine procedure, partial differential equations, for instance, thus transformed into ordinary differential ones; certain terms were omitted; powers neglected. Concerning the above sodium-conductance equation, '[b]etter agreement might have been obtained with a fifth or sixth power', as the nerve-team informed, 'but the improvement was not considered to be worth the additional complication.'[973] Hence a third power: m^3h.

The complexity that the equations assumed, and hence the model, and hence the degree of resolving the impulse into its micro-components with any definition, was a function of what was realizable in practice. 'Describing', then, took on new meanings here: computing. Computational *labour* not computational *metaphors* was essential the reality-effects of this post-war model-cell, and the computational practices Huxley mobilized to actually *realize* the model indeed didn't differ from those discussed in the context of their war-time work. The 'numerical methods' employed were those self-same, algorithmic procedures.[974] And after 1952, it was notably Cole and his assistants in Bethesda who would put considerable efforts into 'checking' and 'testing' these calculations, harnessing initially, SEAC, the electronic computer that had been built at the U.S. National Bureau of Standards in 1950.[975] This was how this model-cell existed; and all the while, its material substrate was 'spreading', as Hodgkin noted:[976] squid giant axons, tracers, electronic assistants and amplifiers weren't scarce commodities in those days.

[973] Ibid., p.509 and passim.
[974] Ibid., pp.523-524.
[975] Cole, Antosiewicz, and Rabinowitz (1955); Miles (1972); more generally on the early uses of computing machinery in the life-sciences, see November (2006): esp. chapter 3.
[976] Hodgkin to Ling, 10 August 1949, HDGKN H.18

Conclusions

This was the new, quantitative life of the cell, in the 1950s: knowable, existing, now as before, only as a model. Its substrate, however, was dispersed now in a world that itself had gradually been turning into one of numbers, electronics, and tracer elements. As a theoretical reconstruction, it formed part of this complex fabric rather than represented it. It integrated and concentrated the new micro-realities of the nervous impulse into a definite, communicable, and certainly enough, physical picture.

No doubt its persuasiveness (to many) derived not least from this feature, the epistemic and ideological virtues it embodied. Influential scientists such as John Eccles belonged to those, as he informed Hodgkin, who now were becoming 'more than ever convinced of the necessity of mathematics for physiology'.[977] Already his 'best students [were] quite authorities on [Hodgkin's] work' and they 'invariably chose the questions relating to electrical and ionic problems of the membrane.'[978]

If these problems delineated the new model-cell, it clearly was not simply about a mere equation or hypothesis, as we have indeed seen. Here was also in the making a role-model of physiological practice, a lead for the post-war world of biology. This work had an almost natural appeal to the growing numbers of model-minded scientists who began to populate the new, electronics-infused borderlands of science for a complex set of reasons – reasons far too complex, of course, to be reduced to 'the war'. We still know very little, however, about these reasons, philosophical, social or otherwise, or the post-war history of cell physiology and nerve science. And what we do know, I have suggested, is problematically biased towards the *discursive*. If the radio-war and its material, mundane dimensions has figured prominently in the above story, it was, not least, to reinforce and make sense of the notion of the 'almost natural'. Throughout this chapter and the last we

[977] Eccles to Hodgkin, 10 June 1949, HDGKN H.15
[978] Eccles to Hodgkin, 20 December 1949, HDGKN H. 18

have seen how the materials of modeling-practice were re-engineered *along* with the materials of the world, including the numerical substrate of the cell itself. It was a world, the argument was, more banal, more everyday, and more extensive than we imagine when we read the history of biology through the lens of intellectual and vocal ruptures, be it an omnipresent information discourse or the cybernetic few.

CONCLUSIONS.

Resurrecting the cell

> *I should like to point out that neurons do many things besides conducting impulses. In fact an embryologist friend of mine feels strongly that impulse conduction is one of the least interesting properties of neurons [laughter].*[979]

The laughter above, provoked by biophysicist Francis Schmitt among those gathering for the third Macy Foundation meeting on the *Nerve Impulse* in 1952, cannot come as a surprise. It betrayed something of the intimate, defining alliance that had been forged between the unit of life – the cell - and its bioelectrical expressions that has been subject of this thesis. Though tongue-in-cheek, Schmitt's embryologist friend certainly had a point in feeling strongly about the matter. Few biological problems arguably shaped visions of the

[979] '3rd Nerve Impulse Conference' (ca. 1952) , MC154, Box 11, Folder 13

biological cell in comparable fashion than this impulse and the problems surrounding it – the nature of cellular surfaces or of permeability changes or that of the electrical structure of cells.[980] Even though, that is, neurons *did* many things besides conducting impulses: growing (tissue culture), emitting chemicals, or being stained, to name only a few and the historically relatively well charted ones.[981]

In entangling the cellular, bioelectrical expressions of life with its models and thus, worlds other and beyond the biological laboratories, this thesis has asked a different question, however. Not what neurons (or more generally, what cells) *did* was central here, but what they *were*.

This thesis has written the story of a formidable, scientific problem - the nature of the cell's bioelectrical behaviours - into the midst of vast, material landscapes and projects - much vaster (and less natural) landscapes than the *nature of life* (or its 'unit') would seem to comprise. In turn, it offered no exhaustive, historical account of the cell or of one its emergent disciplines, be it cell biology, biophysics, molecular biology, or neuroscience. All of these coalesced in decades later than the decades this investigation has concentrated on; or as some argue, much later, as late as the 1980s.[982] But bracketing them here was not only about pre-empting anachronism. In uncovering these more distant landscapes and in following the materials, models, and mundane practices courtesy of which these particular cellular *doings* – impulses, membrane alterations or permeability changes - were manipulable and elucidated *as ersatz*, this thesis has exposed something more fundamentally revealing about the historical *being* of cellular life, and thus, about the history of the life sciences in the twentieth century.

The case of the cell, as argued in this thesis, challenges core narratives that inform

980 See e.g. Ling (1965); Klemm (1972); Trumpler (1997); Pollack (2001); Piccolino (2002); Meunier and Segev (2002); Barbara (2006).

981 On tissue culture, see Billings (1971); Wilson (2005); Landecker (2007); on chemical nerve transmission, see Tansey (1991); Tierney (2001); Valenstein (2005); on staining/histology, see Breidbach (1993); Dierig (1994); E.G. Jones (1999).

982 On this periodization issue, see esp. Wilson and Lancelot (2008).

histories of twentieth century life science. As to the nature of the cellular, fundamental life, instead of molecular dimensions or model organisms, the macroscopic, real-world entanglements of its inanimate models were shown to be vital. They made the cell be 'there' I have argued, in the twentieth century among electrical circuits, colloidal matter and moving bodies. Local, investigative programs, disciplinary agendas, individual scientists, and indeed, *life* science, came in second: it is mundane, fabricated materials and sciences of stuff that emerged as the central agents in this story of the cell. Studying these materials and sciences, it turned out, *was* to study these models. And it *was* to study the biology of the cell. This view has implications - for the history of the life sciences and the history of scientific modeling alike. Let us begin with the more specific first – it has to do with the nerve cell - and then move towards the more general, the historical big pictures of twentieth century science.

1. The nervous system beyond neuroscience

The laughter above, and the occasion – the 1952 *Nerve Impulse* meeting - might very well have stood at the beginning of another chapter or of a different story altogether: it very well might have served as the opening to a - yet unwritten - history of neuroscience in second half of the twentieth century. One would find strong continuities indeed between the scenes and figures subject to this thesis, and what would, beginning in the 1960s, become neuroscience.[983] But this nerve cell - and certainly in the ways that it figured here - has failed to shape our historical sense of the nervous system and that of its incipient science alike: neuroscience.

It was the central nervous system - then as now something much more publicly

[983] The literature on post-war developments is more than scarce, but see Swazey (1975); Brazier (1978); Marshall, Rosenblith, Gloor, Krauthamer, Blakemore, and Cozzens (1996); Cozzens (1997); Farreras, Hannaway, and Harden (eds.) (2004).

visible than the developments charted here - that began to shape discourses surrounding the nervous.[984] There was a 'climate favourable to all fields of research in any degree involving the brain, whether they begin or end with it', as the French electro-physiologist Alfred Fessard diagnosed in 1952, reviewing the case for a projected International Brain Institute under the umbrella of UNESCO. Fessard did not even bother 'to repeat the usual generalities about the importance to mankind of the intensive study of the brain'.[985] In wake of WWII, human behaviour and mental health turned into fundamental problems of planetary dimensions - and vocal scientists of the nervous system turned legion.[986] When Karl Popper's new friend, the neuro-physiologist John Eccles now confidently disclaimed how 'Cartesian primitiveness' had been overcome 'largely by electronic techniques' - so the prelude to his 1952 Wayneflete lectures, *The Neurophysiological Basis of the Mind* - such grandiose statements, however, had a basis usually running no deeper than investigations of squid axons or the cat's neuro-muscular junction.[987]

No doubt, in the 1940s and 1950s, as Hodgkin and Huxley were devising their model of the action potential, many a former scientist of excitable tissue – many among those gathering at the above *Nerve Impulse* meetings included - began to chart somewhat more intricate terrains. In fact, the electronics-based physiology of simple systems and the early adopters of the label 'neuroscience' - Schmitt being one of the most influential ones - were a basically identical community. Their circles defined and delineated a nascent field:[988] Eccles' *Physiology of the nerve cells* (1957), Bullock's *Structure and Function in the Nervous*

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[984] As I have suggested earlier, one historiographical consequence is the next-to-exclusive focus on the brain/mind in historical approaches to the neurosciences.

[985] Fessard (1952); and see nn. (1948).

[986] On these mid-century shifts in discourse, see esp. R. Smith (2001a); R. Smith (2001b). Like the institutional, post-WWII history of neuroscience generally, these developments are barely understood. Arguably, it was then that the brain first emerged as a site of concrete intervention and observation. Formerly an inferred entity, accessed by proxy through the peripheral nervous system or indirectly through clinical observation, post-mortem analysis, and psychiatric practices centring on the body and bodily discipline, the central nervous system – the 'living brain' itself – was turning into an object of experimentation thanks to such innovations as the EEG, electronics, lobotomy or LSD; On the post-war moment of international mental health, see Brody (1998); M. Thomson (1998); M. Thomson (2006).

[987] J.C. Eccles (1953): p.VI.

[988] See esp. Sengupta (1989); Squire (1996); Clarac and Pearlstein (2007).

System of Invertebrates (1965), Katz's *Nerve, Muscle and Synapse* (1966), Schmitt's *The Neurosciences: A study program* (1967), Kuffler's *From Neuron to Brain: A Cellular Approach to the Function of the Nervous System* (1976), or Kandel's *Cellular basis of behavior: an introduction to behavioral neurobiology* (1976) in one way or another gave definition to the coalescing sciences of the nervous system. They did so from the cellular, ionic point-of-view whose articulation has provided the historical horizon of this thesis.

This thesis was not offered as a history of neuroscience. This history - that of the broader circumstances within which the model-cell that Hodgkin, Huxley and their allies had devised unfolded - remains a task for future research. Yet, in charting the development of cell-models, this thesis holds implications, not least, for such a history. Seeing above continuities will require displacing, as the present thesis required it, our brain-centred accounts of what the neuroscience is – and was.[989]

Seen as a history of the nerve cell, the picture presented in this thesis departs significantly from what this history is commonly taken to involve. If muscles, nerve-cells, and bioelectrical potentials here took the place of brains, nerve messages and cybernetic signals, the claim was not, however, that the brain was simply absent and irrelevant from this history. In insisting on the former and in belittling discourses and the excitement surrounding the brain, the aims was not to pit a dull history of dry but 'real' science against a cultural history of the nervous system in the period. It is important to get this positioning right: the case that is being made here is not one against a cultural history, but *for* one. Although today we are prone to identify 'neuro' with brains, writing cultural histories of neuroscience will mean taking more seriously, in ways the present thesis did, the many and material factors besides the brain that shaped the history of the nervous system.[990] In making a case of the peripheral nervous system – the body – as a site of neuro-

[989] In addition to the literature cited, further examples of this genre include Gardner (1985); Corsi (1991); Hagner (ed.) (1999); Weidmann (1999); Kay (2001); Hagner and Borck (eds.) (2001); Dumit (2003); Kevles (1997).

[990] A crucial example pointing towards such non-central directions is the work on nerve gas researches during WWII by historian Schmaltz. See Schmaltz (2005); Schmaltz (2006).

physiological knowledge production, especially chapters 2 and 3 must be seen in this light. Conversely, writing such histories will mean taking more seriously the severely utopian and discursive dimension of the renewed, mid-century scientific excitement about the central nervous system - and not only in terms of cybernetics.[991]

No doubt, the imagined site of the nerve impulse, whether observed in the squid or other such lowly material, then moved definitively into the human brain. But, as this thesis has shown, historically the mundane sources of nervous activity were many, and indeed, lowly. Many of them were unexpected: they were areas seemingly remote from the study of nervous phenomena, let alone, the brain or mind. The history of the nervous system, like that of the cell generally, here revealed itself as a much less brain-centred affair. And being able to see such influential advances as the Hodgkin-Huxley model within a continuum of dispersed and now obscure, mundane forms of biological knowing is one of the significant results of this thesis. These models of bioelectrical activity were something else than a step towards elucidating the mysteries of the brain, mind and its messages.[992] In turn, sites and scenes of knowledge production of the kind that figured in this thesis will remain obscured as long as we equate the history of the nervous system with a history of neuroscience, and neuroscience with brain science.

[991] Historians certainly do take seriously this discursive dimension, but usually by referring the contemporary hype surrounding the neurosciences back to brain-fads of the past. The brain-centredness of past and present discourses, however, goes unquestioned. See esp. Borck (2005); Hagner (2006).

[992] This is a quite typical construction, see Gardner (1985); Kay (2001); Kandel (2006); Christen (2008); Abraham (2006).

2. Big pictures of life science

These sites and scenes did not only sit uneasily with the brain, however. Model-cells and their material substrates, this thesis has shown, explode common narratives and common assumptions made about *life* science. For the most, these models and substrates were not even biological, like *model-organisms* are. Crucially, the cell, on the account presented here, was not simply surpassed by or itself the subject simply of progressive *molecularization*. These are concepts and narratives that have profoundly shaped the received, bigger picture accounts of twentieth century biology. And they have particularly shaped, I have suggested, a theme that looms large in the literature - that of the intersections between physics and biology.

By enrolling the materiality of models into the picture, this thesis presented a novel account of the ways physics and biology intersected in a period that is quite commonly associated with the broad transformation of biological science into a quantitative, experimental and physico-chemical affair.[993] Whether, in the interwar period, students of permeability appropriated the practical knowledge that formed around synthetic products, or whether, in the 1940s and 1950s, electronics, computational labour, and bioelectrical data merged into a re-engineered nervous impulse, the substrate of the cellular life itself was woven, I have shown, from a mundane, worldly fabric. This fabric, significantly, comprised *technical* materials rather than emphatically physical, artificial or non-biological ones. As significantly, it comprised materials that were *pervasive*: useful, fabricated, and known, they traversed the world: semi-synthetics, muscular action, electrical circuitry, numerical things, and electronic scrap. Historically, on this account, cellular *nature* was the

[993] Also see, for instance, Kingsland (1995); Mendelsohn (1998); Erlingsson (2005).

product of mediation processes between models, their materials, and the historical circumstances within which these materials emerged as pressing matters of scientific knowing.

It was in virtue of their mundane and if you will, ontological dimension that they figured as models: ersatz-objects, as concrete, material analogies, as substitutions, and as mediators of the abstract, quantitative substrate of theoretical reconstructions of cellular behaviour. And it was in virtue of these material, mundane entanglements that a form of quantitative, physico-chemical biology coalesced in the sciences of the cell they called up. Intellectual agendas, processes of standardization, even instruments came in quite secondary. Bio/physical transformation and intersection was integral to these entanglements. They were not programmatic.

The process of biology's (intellectual) 'borrowing' from physics or its (technological) 'colonization' by physics revealed itself as a rather subterranean and not particularly optional one.[994] Or rather, in the course of this thesis such demarcations between things non-biological and things biological themselves were demoted. It is an important point. For all their differences, the intuitive notion of biological science that existing accounts and approaches share - of where and how it happens and of the factors that shape it – this thesis has shown to be limited, perhaps even somewhat overly romantic. And it was not only materiality as such that mattered in this connection. 'Bio-physical' science - whether Hill's muscular physiology, William Bate Hardy's low-temperature science of food-stuffs or Kenneth Cole's medico-physical forays into the fundamentals of nervous action - here made its appearance not, as available treatments of biophysical developments typically suggest, as a matter exclusively of academic discipline building or interdisciplinary venture.[995] They can be seen, this thesis has shown, as epiphenomena of practical relations – practices forming at the margins of thing-based and utterly practical and routine

[994] On these terms see esp. Garland E. Allen (1975); resp. Abir-Am (1984).
[995] See, for instance, Abir-Am (1987); Kohler (1991); Rasmussen (1997b); Abir-Am (2003).

scientific activities.[996]

Yet against the background of these practice-bound incarnations of biophysics, existing accounts appear as built around public visibility as much as historical significance.[997] The image, for instance, of the intimate association between progressive (read: experimental and physico-chemical) biology and progressive, leftist outsider politics that informs accounts of interwar British biology in particular,[998] appears no less problematic in this light than the significant amount of historical attention that has been devoted to the biophysical musings of physicists such as Bohr, Schroedinger or Jordan.[999] What is missing from these stories are the far less visible but sizeable formations – well before WWII - such as colloid science or (applied) physiology. They, rather than intellectual agendas and positions, shaped the borderlands of physics and biomedicine. And more than anything else, these formations, we have seen, centred on the cell.

Second therefore, in resurrecting cells by way of models and materials, this thesis has shown that *molecularization* is a category more problematic and a factor less central to biology's physico-chemical transformations than big picture accounts typically imply. The cell was and remained central, we have seen, to shaping biological investigations. And yet, it was not simply the case that *molecularization*, and the narratives associated with it, tend to obstruct from view what was a vast realm of investigations in itself. They also tend to obstruct the sort of macro-cosmic entanglements which featured prominently in the foregoing.[1000]

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[996] The protagonists that featured in the five preceding chapters indeed are not easily subsumed into one neat category. What they had in common generally was not a specific discipline, locality, training or other, intimate social bonds. For many of them, the fundamentals of bioelectricity were not even much of an issue whatsoever. What they all had in common, and this is why they appeared quite prominently in this account, was a certain technical, physical outlook on the problems of biology they encountered in their daily, routine practice.

[997] The problems of biology that were comprised in colloid science, industrial physiology or medical physics – mundane borderlands of biology and physics - themselves were precipitated, as we have seen, by nationalist, economic factors and material forces that frequently operated well beyond academia, local research cultures, intellectual programmes, and particular institutions.

[998] Abir-Am (1987); Mazumdar (1992); A. Brown (2005); Erlingsson (2005); also see Werskey (1978).

[999] See esp. Kay (1985); Beyler (1996); Aaserud (2003); McKaughan (2005).

[1000] Here, even when molecules did enter the story, as was the case notably with the bimolecular model of the cell surface (chapter 1), these molecular dimensions turned out to be mediated by a much richer set of

In obstructing these entanglements, molecularization-narratives imply dynamics of historical change that capture narrow parts at best of what were the historical, mundane realities. Indeed, not only the cell was so entangled: the intimate relationships that formed between say protein biology, x-ray crystallography and interwar textiles and fibre research are - in principle - well known.[1001] But it is, notably, the 'new physics' that systematically shaped the story of molecular biology, embodied in visionary figures such as Delbrück, Schroedinger or Pauling. The much more established applications of classical thermodynamics and physical chemistry – products, like the cell, of the nineteenth century – hardly feature at all. Consequently, neither do the kind of 'fundamental' investigations into material, man-made things that were examined here.[1002] In short, the material agents of historical change exposed by this thesis were more anonymous, more encompassing, more cell-centred - and less biological and progressive - than the received big picture allows.

3. The normalcy of modeling

We need to adjust our historical understandings of what the objects of biological knowing were, certainly in terms of the cell. Once we had put them back into their historical, material surroundings, cells, artificial models and modeling practices themselves appeared as nothing peculiar or particularly exotic. And it was this *normalcy* that pointed beyond this particular object – the cell - and towards the historiography of twentieth century science, generally. Exposing this *normalcy* meant to question the overarching narratives of twentieth century science into which we tend to inscribe scientific modeling-practices.

Historians of science, of course, have already exploded the category – model - into

macroscopic things – soaps, surface films and vitamin D, for instance.

1001 See esp. Berol (2000); Wilkins (1987); P. Harris (2001).

1002 On the relevant notion of 'fundamental' (as opposed to 'pure') research, see esp. S. Clarke (2006); S. Clarke (2009).

a myriad different cases and uses.[1003] But the grand narrative of models is a different one. Frequently dated at mid-century, it is a narrative of incision revolving around the post-WWII moment of interdisciplinarity, cybernetics, the impact of digital computers, or information theory.[1004] In putting the materiality of models centre-stage, this thesis systematically diverged from the ways scientific models have figured in historical analyses.[1005] When we look at (and around) the cell, modeling-practices were nothing new, exciting or unusual by 1950. Digital computer simulations and model organisms, as the largely post-mid-century technologies that inform much of the recent surge of historical interrogations of models in science indeed appear as much more particularistic practices from this perspective.[1006] Likewise, the obsession with logic, language, representation, and scientific method that formed part of the epistemic meta-discourse on models that was being generated at the time by cybernetic intellectuals, philosophically-minded scientists, and philosophers of science such as Mary Hesse, George Canguilhem, and Max Black here made its appearance at the margins at best - and certainly not as unproblematic and historically transparent, analytical concepts.[1007] Substitutions not representations, concrete not discursive, the models at issue here were integral to the material fabric of scientists' life-worlds, entangled and emergent from scientific activities that themselves were coalescing around rather mundane things. Re-construing modeling practices this way – re-aligning them, that is, with a spectrum of materials-based knowledges - meant to question

[1003] From dioramas to war games, from 'blood drill' army-training realism to war-games to wax-models in embryology, wind tunnels, analogue computers, flight trainers, and war – all these things can be and, more significantly, have historically been considered as types of models, simulations, and essential strategies of knowledge production. They could be matters of pedagogy, popular instruction, predicting and getting things done; nothing particularly logic, formal, or immaterial. See, for instance, Lenoir (2000); Bourke (2001); Chadarevian and Hopwood (eds.) (2004); Light (2008).

[1004] Examples include Heims (1980); Galison (1994); Cohen-Cole (2003); Siegelman and Flo Conway (2004); Crowther-Heyck (2005); Boden (2006); Daston and Galison (2007); Wheeler, Husbands, and Holland (eds.) (2007); but see Wright (2003); and Kline (2009).

[1005] It was, for instance, not the abstract quality of 3-dimensionality that was particularly important here. On the 3-dimensionality of models, see Chadarevian and Hopwood (eds.) (2004).

[1006] See esp. Edwards (1997); Edwards (2000); Cordeschi (2002); Fox-Keller (2002); Wise (ed.)(2004); Crowther-Heyck (2005); Boden (2006); November (2006); Creager, Lunbeck, and Wise (eds.) (2007); W. Thomas and L. Williams (2009).

[1007] See, for instance, Rosenblueth and Wiener (1945); J.Z. Young (1951); Rothschuh (1952); Walter (1953a); Walter (1953b); Beckner (1959); nn. (1960); Black (1962); Hesse (1963); Canguilhem (1963); generally, on the cold-war/philosophy of science nexus see esp. Fuller (2000); Reisch (2005).

the elements comprised in the standard narrative.

We cannot simply rely, this analysis suggested, on the cybernetic scenes and registers to frame our historical accounts of the nervous system and its models in this period. In terms of models especially, there was continuity and expansion rather than incision. As much as we have seen, in each chapter, quantitative, technical, physico-chemical biology form around common things and practices, chronologically, the move towards formal and abstract models in the 1940s and 1950s itself could be construed as the intensification of such mediation processes.

Unlike the more familiar exemplars - the telegraphy *metaphor* for the nervous system, for instance – these inconspicuous modelisations of the cellular life were firmly grounded in a mundane ontology of things, not in the *discourses*, verbal and textual. And they made this account an historical rather than epistemic or philosophical one. This thesis indeed raised questions about the complexity of the transformations at stake in this period. A historical understanding will depend, as this analysis also suggested, on breaking up the homogeneity of present perspectives (such as 'information discourse'), and on looking more closely and simultaneously at the various shifts in and interactions between discourses, epistemologies, practices and material cultures of modeling. From a rather different angle than the recent work by Jamie Cohen-Cole on the cold-war, normative constructions of the model-minded mind within cognitive psychology, especially the chapters on *Numbers* and *Electronics* thus have thrown into relief the ways in which a vulgar psychology and philosophy of models must be seen as co-emerging with changes in modeling practice, not as representing it.[1008]

It is historical visibility, in other words, rather than historical realities that has informed much of our historical sense of models. And the assumptions historians have built into the standard narrative tend to reflect it. Where this account significantly diverged

[1008] Cohen-Cole's work is arguably the most systematic attempt at historicizing modeling-practices available. See esp. Cohen-Cole (2003).

even from Cohen-Cole's otherwise more than overdue push towards historization is a matter of historical perspective. Cohen-Cole's concern is the solely cold-war period, and like other studies concentrating on the period, it encompasses a view of models, notably, as mediators of interdisciplinary – *academic* – research.[1009] But, as the case of cell-models demonstrates, embracing too emphatically the picture of models as cold-war agents of interdisciplinarity (or vice versa), is to get things backwards. In this material story of the cell - though each chapter did engage with forms of scientific activity which were evidently *not* disciplined-based - both 'interdisciplinarity' and 'models' were epiphenomena of far less remarkable sciences of stuff. We may identify them as such (the former), but the emphasis was and should be on something else (the latter): the normalcy of such arrangements. Historically, that is to say, we cannot treat interdisciplinarity uncritically as progressive, desirable, laudable, without precedent - the almost natural, recent progression of knowledge and the discipline-based order of science of the past.[1010]

As this thesis has shown, it was too normal and too routine to deserve such treatment - even in the academic realm.[1011] But the more general point is this: disciplines, borderland science or interdisciplinarity are categories taken from the world of academic science, rather than science, conceived inclusively. Taking the academic discipline as the analytical unit would have obscured rather than illuminated the nature of the thing-based scientific practices and formations that have been at issue here. It is, in fact, a significant shift of perspectives: on the present account these formations emerged as much more productive and relevant than previous accounts of interwar biophysics, colloid science or general physiology had allowed.[1012]

[1009] See esp. Cohen-Cole (2007); the same tendency is palpable, for instance, in Creager, Lunbeck, and Wise (eds.) (2007); Mattila (2005); Loettgers (2007); Barnes (2008); A. Johnson (2009).

[1010] Werskey (1978); Abir-Am (1987); Galison (1990); Abir-Am (2003); Anker (2005); A. Brown (2005).

[1011] 'Team work', organized, and collaborative research, too, as historians such as Clarke, Hull, Cooter and Sturdy indeed have argued, had become a fairly routine affair in Britain after the Great War, not least, as far as government-sponsored, civilian biomedical science was concerned. In the U.S. too, collaborative (civilian) research and 'borderland sciences' were fostered by a great many, fairly establishment agencies in the New Deal era; Nazis could be as enthusiastic about it as communists or the scientific friends of Bauhaus. See esp. Bugos (1989); S. Clarke (2006); Sturdy and Cooter (1998); Galison (1990); Hull (2007).

[1012] Kohler (1975); Kohler (1982); Servos (1982); Pauly (1987); Servos (1990); Kohler (1991). There were no

These formations were, as this thesis has shown, productive indeed. There was produced, among them and in the midst of the man-made materials that connected them, the *living* cell. Or more properly, it was a continuum of fabricated, processed and macrocosmic things - a continuum of the 'artificial' and the 'natural' - that mediated the microcosmic nature of the living cell. It is a picture of knowledge production that would seem to be far less reminiscent of the rational images of scientific modeling philosophers of science used to concoct – quasi-linguistic, logic formalisms - than it is reminiscent of the Renaissance *Order of* Things à la Foucault, or a kind of twentieth century *wunderkammer*.[1013] Science, at any rate, knew the cell mainly by diverted means. Science knew it, I have argued, through something else, something that was not exactly natural but fabricated, processed and hence, already understood in some way or the other – through things such as athletic activity, electrical circuitry or artificial films.

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disciplinary 'failures': institutional success or not, these are not, this thesis has shown, the appropriate questions to ask when it comes to investigating the productivity of this or that grouping of scientists, however transient, ill-defined, and transitory. Such labels as biophysics in turn here functioned as descriptive and heuristic terms only. What they are, in a given case, is largely an empirical question. Materials and concrete, practical relations go a long way to account for the transitory stability of a domain of inquiry.

[1013] On Foucault's ideas on the analogical episteme, see Foucault (1970); on wunderkammern, see Daston and K. Park (1998); and on the long long history of the artificial/natural theme, see, for instance, Bensaude-Vincent and Newman (eds.) (2007).

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