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The Brain Electric: A History of Neuroscientific Ideas About How We Change

^{by} Cristina Nigro

DISSERTATION Submitted in partial satisfaction of the requirements for degree of DOCTOR OF PHILOSOPHY

in

History of Health Sciences

in the

GRADUATE DIVISION of the UNIVERSITY OF CALIFORNIA, SAN FRANCISCO

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by

Cristina Nigro

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The Brain Electric: A History of Neuroscientific Ideas About How We Change Cristina Nigro

Abstract

This dissertation examines the historical context of nineteenth- and twentieth-century neurophysiological ideas and experiments. It uses archival records and correspondence, primary scientific literature, and secondary materials to explain and interpret the origins of contemporary neuroscience and, concurrently, explains and interprets modern ideas of the self. It analyzes nineteenth-century investigations into the nature of the nervous impulse via the examination of the laws of electrical activity as part of new formulations of natural law and the natural order. It demonstrates how nineteenth-century neurophysiological findings and interpretations were shaped by discoveries in electromagnetism and thermodynamics and must be understood through philosophical and evolutionary discourse. Twentieth-century neurophysiologists made the electroconductive model of nervous system functionality axiomatic through the methods and tools of reductive experimentation and analysis which depended on instrumentation developed for industrial and military purposes. Psychologists, cyberneticists, and modelers of neural computation engaged with neurophysiological research and concepts to create new theories and frameworks of functionality which took for granted the notion of the nervous system as continuously active, temporally dynamic, finely regulated, and incessantly adapting. A neuropsychological theory from the mid-twentieth century conceived of human behavior and cognition as the integration of neural activity which preserved permanency yet allowed for

generalization through neurophysiological processes of learning and remembering. Neural modelers mechanized the notion of human cognition as distributed across networks of neurons that are continuously changing into themselves. By investigating neurophysiological research and concepts from the mid-nineteenth to the late twentieth centuries, this dissertation reveals the fundamental ideas, experimental approaches, and physical tools that continue to shape how we make sense of ourselves.

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Introduction

Having trained in psychology during the interwar years, the Canadian neuropsychologist Donald Hebb (1904-1985) began to pen his crowning achievement as the mid-twentieth century approached. His written work, The Organization of Behavior, contributed to a larger and longstanding conversation about the role of nature versus nurture in the configuration of the self and resulted in an original formulation of the dynamic relationship between brain and mind. It contained Hebb's theory of the cell assembly, a notion understood by twenty-first-century neuroscientists as the forerunner to modern conceptions of synaptic plasticity—the idea that activity-generated physical alterations in the connections between brain cells, or neurons, leads to lasting neurobiological and mental change. According to Hebb, a cell assembly forms when a particular stimulus drives a diffuse network of neurons to act together as a closed system and, through its temporally-associated activity, facilitates activity in other such systems. Hebb's theory posited that cell assemblies actuate as modifications in synaptic connections within the system and provided a testable working hypothesis for interrogating the link between mental activity and neurophysiological activity. Anyone with training in the neurosciences knows the Hebbian adage: neurons that fire together, wire together.

Hebb built his theory on the backbone of the electroconductive model of nervous system functionality, a model developed and refined over more than a century. In the 1840s, the German physiologist Emil du Bois-Reymond (1818-1896), following from the new science of electrodynamics studied by physicists, observed the action current in excised nerve-muscle

preparations of frogs' legs, and described the action current as an altered state of the nerve. The action current, known today as the action potential, or colloquially, when a neuron "fires," is the change in electric current observed during neuronal activity.

Du Bois-Reymond lived and worked in an era of German dominance in physiological inquiry. His investigations, along with those of his famous friend and colleague, the German physiologist Hermann von Helmholtz (1821-1894), were outgrowths of the early nineteenthcentury move to make biology more "scientific." Centered at German universities, experimental physiology was seen as the model of the experimental method. German physiological laboratories, drawing from concepts originating mostly in France, became the place where physiology as a scientific discipline gained its independence from the study of medicine. A distinctly German approach to experimental physiology included the adoption of tools derived from the study of physics, like the galvanometer, a penchant for quantification and graphical representation, and the use of isolated organic preparations like the excised frog leg du Bois-Reymond employed in his nerve and muscle research. By the end of the century, physiological laboratories cropping up in Britain, the United States, and France, mimicked the German model.¹

Du Bois-Reymond and Helmholtz, representatives of the German model, sought to distance themselves from earlier German natural philosophers who insisted on explaining organic life as governed by vital forces which could not be reduced to physicochemical entities. Avowed materialists, du Bois-Reymond and Helmholtz rejected notions of teleological reasoning in physiological investigation. They claimed to be interested only in physical explanations of cause and effect, which assumed time as an independent variable in physiological functioning. This dissertation, however, places du Bois-Reymond at the center of an emerging intellectual

¹ Kremer, Richard L. "Physiology." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences.* Edited by Peter J. Bowler and John V. Pickstone, 342-366. Cambridge: Cambridge University Press, 2009.

tradition of viewing the process of understanding as historical progress. It argues du Bois-Reymond's functional study of the frog nerve-muscle preparation depended on the arrival of a dynamic conception of the natural order, which placed materiality and ideation as inherently and temporally intertwined. His interpretation of the action current as an altered state of the nerve allowed for a meaningful physical basis of change in living beings.

Helmholtz, meanwhile, paved the way for investigations in understanding nervous conduction through the lens of energy transformation and the first law of thermodynamics. His discovery of the speed of nervous conduction coincided with nineteenth-century debates about evolution and physiological time. Helmholtz served as a crucial link between German and British science in the nineteenth century.

Post Darwin, British physiologists, in contrast to German physiologists, incorporated evolutionary explanations into their physiological interpretations. The English physiologist Michael Foster (1836-1907) headed the premier experimental physiology laboratory of the late Victorian era at the University of Cambridge, and his focus on correlating structure with function in evolutionary terms was emulated by the English neurophysiologist Charles Sherrington (1857-1952) and his colleagues.² Sherrington featured as second author for the 1897 seventh edition of Foster's widely-read *A Textbook of Physiology* in which Sherrington introduced the word "synapsis."³

Having accepted evolution as a driver of change, the question for British physiologists at the turn of the century remained—what is the mechanism of that change? Following from the

² Kremer, Richard L. "Physiology." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences*. Edited by Peter J. Bowler and John V. Pickstone, 342-366. Cambridge: Cambridge University Press, 2009, p. 353. See also, Geison, Gerald. *Michael Foster and the Cambridge School of Physiology*. Cambridge: Cambridge University Press, 1978.

³ Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs of Fellows of the Royal Society*, 8;12(1952):241-270, p. 248.

Germans, including the work of du Bois-Reymond's which positioned moving electric current as a proxy of neurophysiological change, early twentieth-century neurophysiologists doubled down on materialism and reductionism, reasoning that looking at the nervous system at the level of its basic functional units—neurons—would lead to the answer of what constituted the self. By midcentury, neurophysiologists agreed with certainty that electrical changes accompanied nervous activity. Attention to temporality was integral to understanding nervous and mental activity, as were the interrelated guiding principles of regulation, order, and action.

Underwritten by the taken-for-granted neurophysiological fact that the nervous system transmits information via electroconductance, Hebb conceived of his theory in response to a perceived disconnect between psychological theory and physiological observation. From Hebb's perspective, the behaviorists, through their striving for objectivity in psychological inquiry and in their self-conscious desire to mimic the reductionist, data-driven sciences, lost sight of where the meaningful action really occurs—in that black box between external stimulus and behavioral output. According to Hebb, the anti-reductionist Gestalt psychological theory of wholes as more than the sum of their parts, failed to adequately account for physiological fact. Hebb reasoned that there might be multiple physiological variables which could accomplish the same behavioral output and that nervous activity could transmit along multiple pathways, which might change themselves.

Synthetic histories of modern physiology tend to concentrate on the nineteenth century, when physiology as a discipline separated from the study of medicine, first in France and Germany and soon after in the U.K. and the U.S. These histories, which began to appear in the 1950s and 1960s when the history and sociology of science became professional disciplines in

their own right, emphasized four prominent themes: physiology's fight for independence from medicine, physiologists' embrace of the experimental method (and, correspondingly, a rejection of nonempirical views to understanding life), the impact of physiological concepts in organizing scientific knowledge production, and differing national traditions and styles of physiological investigation. In the last thirty years, the scope of the histories of physiology have narrowed and, following from a disciplinary trend among historians of science, incorporated external economic, social, cultural, and gendered factors, to name a few, into heterogeneous historical investigations of physiological practices. As a consequence, combined with the fact that in the twentieth century physiology refigured into a way of thinking and doing that crossed disciplinary boundaries rather than standing alone as a general field of study, there is a dearth of synthetic histories of twentieth-century physiology.⁴

In the 1970s, histories of psychology shifted from being generally celebratory to being generally critical of the field and its application to society, succeeding the professionalization of the history of psychology in the 1960s and the influence of the sociology of science on the methodological approaches to the history of science. For example, histories of psychology produced in the 1920s and 1930s compared and contrasted the many schools of psychology and centered on the ideas of "great men," whereas histories produced in the 1980s featured the contributions of women and underrepresented groups and questioned the accounts of earlier histories that placed the official founding of psychology in the nineteenth century.⁵

 ⁴ Kremer, Richard L. "Physiology." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences*. Edited by Peter J. Bowler and John V. Pickstone, 342-366. Cambridge: Cambridge University Press, 2009.
 ⁵ Brock, Adrian. "History of the History of Psychology." In *Oxford Research Encyclopedia of Psychology*. Oxford University Press, 2020, https://oxfordre-

com.proxy.library.upenn.edu/psychology/view/10.1093/acrefore/9780190236557.001.0001/acrefore-9780190236557-e-464; Capshew, James H. "A History of Psychology Since 1945: A North American Review." In *A Historiography of the Modern Social Sciences*. Edited by Roger E. Backhouse and Philippe Fontaine, 144-182. New York: Cambridge University Press, 2014; Fierro, Catriel et al. "Science and Technology Studies and the Historiography of Psychology: Towards a Critical Analysis." *Trends in Psychology*, 27;4(2019):943-959; Watrin,

The history of neuroscience has not undergone a professionalization akin to the history of psychology, which is reflected in the relatively small number of historians and scientists contributing to the canon. A handful of encyclopedic accounts (e.g., Stanley Finger's Origins of Neuroscience: A History of Explorations into Brain Function) attempt to chart the history of neuroscience from its ancient origins, but most stop at or before the early twentieth century, with few exceptions (e.g., Gordon Shepherd's Creating Modern Neuroscience: The Revolutionary 1950s).⁶ Several recent biographies spotlight famous nineteenth-century researchers and their neuroscientific discoveries (e.g., Gabriel Finkelstein's Emil du Bois-Reymond: Neuroscience, Self and Society in Nineteenth-Century Germany, Michel Meulders' Helmholtz: From Enlightenment to Neuroscience, and Paolo Mazzarello's Golgi: A Biography of the Founder of *Modern Neuroscience*), which complement synthetic histories of nineteenth-century neuroscientific investigation (e.g., Mary Brazier's A History of Neurophysiology in the 19th Century and Edwin Clarke and L. S. Jacyna's Nineteenth-Century Origins of Neuroscientific Concepts).7 Autobiographies and memoirs from twentieth-century neuroscientists (e.g., The History of Neuroscience in Autobiography, edited by Larry Squire and Thomas Albright) help to fill in the gaps where synthetic histories are lacking.⁸

⁷ Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013; Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience.* Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010; Mazzarello, Paolo. *Golgi: A Biography of the Founder of Modern Neuroscience.* New York: Oxford University Press, 2010; Brazier, Mary A. B. *A History of Neurophysiology in the 19th Century.* New York: Raven Press, 1987; Clarke, Edwin, and L.S. Jacyna. *Nineteenth-Century Origins of Neuroscientific Concepts.* Berkeley: University of California Press, 1987.

João Paulo. "The Ambiguous "New History of Psychology": New Questions for Brock (2017)." *History of Psychology*, 20;2(2017):225-237.

⁶ Finger, Stanley. Origins of Neuroscience: A History of Explorations into Brain Function. New York: Oxford University Press, 2001; Shepherd, Gordon M. Creating Modern Neuroscience: The Revolutionary 1950s. New York: Oxford University Press, 2010.

⁸ Squire, Larry R. (ed.). *The History of Neuroscience in Autobiography*. Volumes 1-8. Washington, DC: Society for Neuroscience, 1996-2014; Squire, Larry R., and Thomas D. Albright. (eds.). *The History of Neuroscience in Autobiography*. Volumes 9-11. Washington, DC: Society for Neuroscience, 2016-2020.

The electrophysiological study of cognition lies at the heart of contemporary neuroscience, but there has been little historical analysis of its origins and development. This dissertation addresses that historiographic gap. It examines how nineteenth- and twentiethcentury neurophysiologists constructed, legitimized and challenged scientific knowledge, produced new technologies and modified old concepts, helped merge the physical, psychological, and biological sciences, and co-created meanings of the self as part of broader sociocultural, philosophical, and scientific discourse. It also explains how theories about nerve cell activity connect with socio-scientific concepts of intelligence and cognition.

In the mid-twentieth century, Hebb helped redefine cognition as fundamentally a process of learning. A brain without proper adaptive learning or remembering mechanisms, therefore, is an inadequate brain. By revealing how 150 years of scientific research in neurophysiology has shaped contemporary notions of the brain, mind, and corresponding self as constantly changing—as incessantly coming into itself—this dissertation opens up a space for thinking about how stigmas surrounding people with cognitive impairments (like dementia, for example) must be understood within the electroconductive framework of nervous system functionality that scientists have helped cement. The neurophysiologically-shaped notion of the "normal" brain and the "acceptable" self is one that is in a continuous state of becoming. Indeed, a state of becoming was embedded as the fundamental framework of late twentieth-century neural models. A self that is static, inactive, not adapting nor evolving, is not a self at all.

Outline of the dissertation

This dissertation, an intellectual history of neurophysiology and its intersections with sociocultural, philosophical, and scientific discourse about cognition and the self, examines the history of studying the nervous system as a dynamic system from the mid-nineteenth to the late

twentieth centuries. It traces the intersections between theory and experiment and links neuroscience with philosophy, physics, psychology, information theory, and computer science, presenting an original contribution to the history of the science of the self. Understanding evolutionary forces as progressing toward an optimized human being, neurophysiologicallyinspired scholars of the twentieth century advocated ideas of the self as oriented toward incessant enhancement which were underwritten by the electroconductive model of nervous system functionality.

Chapter 1 argues that a functional study of the nervous system depended on the acceptance of a dynamic conception of the natural order in the mid-nineteenth century, an important first step to thinking about the biological basis of learning and memory in the twentieth century. The chapter situates the German physiologist Emil du Bois-Reymond's peripolar model of the nerve's electromotive force within the history of galvanism, the application of electricity to understanding life processes, and the history of electromagnetism, which shaped du Bois-Reymond's explanation of a theoretical causal mechanism underlying the movement of electric current through nerve and muscle. His model maintained the German *Naturphilosophie* imperative for revealing nature's unity of opposites and served as an explanatory prototype for how nerves can materially express change from a previous state.

Chapter 2 examines the physiological research of mid-nineteenth-century German physicist and physiologist Hermann von Helmholtz. Helmholtz's measurements of nerve fiber conduction speed fit in with his project to prove a conservation of energy in organic life processes. Helmholtz and the British mathematical physicist and engineer William Thomson were part of a debate about time and epistemology which subsequently transformed discussion about organic nature via the investigation of the history of the earth and the foundations of

geology. Studies using thermodynamic principles to explain the biological natural order and geological natural order interacted to produce a theory of the evolution of species on the basis of natural selection. Darwinian evolution allowed for an acceptable version of organic teleological progress; the notion of evolutionary time prefigured biology and provided an explanatory mechanism for adaptive nature.

Chapter 3 begins with the English neurophysiologist Charles Sherrington's 1906 *Integrative Action of the Nervous System*, which represents the dominant theoretical and research paradigm in the early twentieth century. The chapter asks how Sherrington's model of the nervous system as an active integrator of information through synaptic connections and coordination of simple reflexes to create complex behaviors and their psychical adjuncts incorporated Darwinian teleology and mechanistic materialism into a conception of a dynamically active nervous system coordinated through its varied temporal relations, yet along stable reflex routes. Focusing on the neuron as the fundamental unit of functional activity, Sherrington and his contemporaries used metaphors of Darwinian adaptation, concepts from the science of energy, and devices made available from new developments in wireless telegraphy to carry out their research program.

Chapter 4 brings to light the historical and intellectual contexts which allowed for the Canadian neuropsychologist Donald Hebb to postulate on the function of dynamic cell assemblies as the neurophysiological basis of learning in his 1949 work *The Organization of Behavior*, which presented new avenues for understanding and examining the biological basis of memory at both the circuit and synaptic levels. Hebb's work opened up a space for neurophysiologists to reconsider their focus on the single cell as the fundamental unit of brain activity. At midcentury neurophysiologists began to look to circuits as the way to understand

how the brain dynamically learns by altering the morphology of synapses and neural connections previously thought to be stable.

Chapter 5 uncovers the historical relationship between neurophysiology, cybernetics, information theory, and computer science through conceptual and research intersections stemming from Hebb's connectionist network theory, experiments inspired by Pavlovian conditioning, research on predictive feedback mechanisms, and neuronal modeling by neurophysiologists and cyberneticians like Warren McCulloch and Walter Pitts at midcentury and the parallel distributed processing group in the 1980s.

This dissertation attempts to track the historical trajectory, from the mid-nineteenth to late twentieth century, of the field of neurophysiology and its connections to generalized conceptualizations of self-identity. This work engages with the work of scientists and scholars, often with their wives beside them in the laboratory (yet invisible in the historical record), from Germany, the United Kingdom, Ireland, France, Spain, Italy, Greece, Denmark, Austria, Hungary, Russia, the United States, Canada, Mexico, Chile, South Africa, and references scholarship from Japan. It is in conversation with histories of neurology, psychiatry, psychology, physics, chemistry, biology, and physiology, as well as with narratives of sickness and health, the philosophy of mind, existential phenomenology, computer science and engineering, artificial intelligence research, bioethics and neuroethics, and the lived experiences of people existing within the current sociocultural milieu of the Western world.

This dissertation attends to changing research paradigms through an investigation of original research monographs and papers of scientists as well as their correspondence and unpublished drafts held at various archival collections in England, Canada, and the U.S. It also examines conference proceedings from the end of the nineteenth to the mid-twentieth centuries.

The dissertation begins to explore how, and in what context, the field of neurophysiology both reflects and shapes changing cultural discourse about how the self relates to the brain and the self's capacity—and obligation—to actively adapt to a changing environment.

The history of neurophysiology serves as a lens to view how people embedded in Western culture understand themselves and their place within the natural order. Western scientists and scholars of the nineteenth and twentieth centuries—who were overwhelmingly white, male, economically secure, and socially well-connected—turned to neurophysiological research and interpretation because they hoped to find the keys to understanding the relation between the brain and mind, the organism and the external environment, as well as the past, present, and future, reduced to a physicochemical level. Through their scientific endeavors, they concurrently imparted ingrained understandings of the natural order and what it means to be human into neurophysiological fact and theorizing. By studying the history of neurophysiology from the mid-nineteenth to the late twentieth centuries, this dissertation attempts to bring to light the fundamental assumptions, ideas, concepts, experimental designs, and physical tools that continue to shape how we make sense of ourselves.

The history of neurophysiology also illustrates how the development of new devices for experimentation and analysis made neurophysiology research possible. Interrogation of du Bois-Reymond's experiments on electromotive force, as one example, reveals the dependent relationship of neurophysiology research on physical devices and analytical tools for observing the nervous system and interpreting its function. The devices and tools used in neurophysiological investigation, therefore, profoundly shaped the kinds of questions neuroscience researchers asked as well as the ways in which they represented neuroscientific knowledge. Apparatuses borrowed from the field of physics, especially those developed

alongside the emergence of the study of electromagnetism and thermodynamics, provided neurophysiologists with the precision and amplification that were originally meant for industrial and military endeavors. Despite its close ties to developments in physics, however, neurophysiology has a unique relationship to what it means to be human. The ongoing tension between reductionism and holism reveals the history of neurophysiology as a necessary forum for studying the contextually-defined laws of human nature.

Chapter 1

An historical epistemology of Du Bois-Reymond's neurophysiology

The German physiologist Emil du Bois-Reymond's (1818-1896) experiments on the electromotive force in frog nerves and muscles were instrumental to laying the foundations of modern neurophysiology.⁹ His studies revealed the new epistemology that emerged out of nineteenth-century electrodynamics and galvanism, which centered on the idea of dynamic change represented materially. His discovery of the action current, which was in conversation with the mainstream physics of the day, provided initial insight into the temporal relations of neurophysiological processes and made possible the idea of change over time as inherent to nervous system functionality. This chapter tells the story of the historical and philosophical context which made du Bois-Reymond's ideas and experiments possible.

With his dynamic philosophy of transcendental idealism, Immanuel Kant (1724-1804) believed he solved the problem of causality raised by skeptics like David Hume (1711-1776). One way we can establish certainty of causation, said Kant, is by understanding the dynamic spatiotemporal relations between interdependent objects—we use our intuitive notion of temporality, for example, as a way to make sense of the world. Time is a concept of the intuition, he said, not a thing-in-itself; it is a way for us to understand how causes and effects are linked

⁹ Typescript of "Two Centuries of Neuroscience: A Brief Survey from Beginnings to Present Trends," Lecture for Wellcome Symposium on Historical Aspects of Neurosciences, April 19, 1991, Box 55, Folder F.67, Bernard Katz papers, University College London, London, England. Katz did not deliver the lecture at the Wellcome Symposium due to ill health. Katz won the Nobel Prize for his neurophysiological researches in 1970.

together. Understanding causation is understanding that substances can change over time, and that they can change each other.

Kant's dynamic philosophy reverberated across Western intellectual circles, shaping particularly the experiments and thought of nineteenth-century physicists and philosophers, whose efforts further shaped the worldview and research programs of generations succeeding them. Du Bois-Reymond's studies of the action current in the nerve-muscle preparation of the frog leg represented an epistemological shift in thinking about the function of the nervous system at midcentury. His theory that changing electrical activity in nerves causes muscular contractions became possible after Kant's dynamic philosophy inspired fellow German philosopher Friedrich Wilhelm Joseph Schelling's (1775-1854) *Naturphilosophie*, with its insistence on polarity as underlying the universal force in nature. Schelling's philosophy in turn shaped the sciences of galvanism and electrodynamics as well as his compatriot Georg Wilhelm Friedrich Hegel's (1770-1831) conceptualization of becoming through the dialectic.

About the same time historical progression became a lens through which to understand both humans and nature, Western European philosophers, physicists, physiologists, and biologists articulated a vision of nature and consciousness which implied the possibility of changing human nature by invoking temporality in novel ways. Thinking about biological life in terms of matter in motion allowed du Bois-Reymond to explain physiological change over time in material terms. Despite declaring it so in his 1847 materialist manifesto and 1848 *Untersuchungen über Thierische Elektricität* which described his nerve-muscle experiments, du Bois-Reymond's materialism was not a complete break from German Romanticism and idealism. Rather, his ideas were shaped by them. Experimenting with galvanism and electrodynamics

The physical sciences veered toward dynamic concerns in the nineteenth century as evidenced by the emerging theory of electromagnetism, which was born earlier in that century. Physicists increasingly evoked the dynamics of interactive forces to explain electrical and magnetic phenomena, moving away from the atomistic, mechanical (i.e., Laplacian-Newtonian) tradition which conceived of molecules acting at a distance in order to explain how a body moved without having touched or collided into another.¹⁰ Electromagnetic theory in the nineteenth century demonstrates the blurred boundaries between dynamism and mechanism at that time. Proponents wrote in terms of Kantian dynamic forces inherent in matter, but some assumed the presence of real, physical entities not accessible to observation; to others, these entities served only as analogies and aids in reasoning.¹¹

The groundwork for electromagnetic theory began the century prior with the science of electricity. In the eighteenth century, experimenters of electricity studied static electric charge, demonstrating its ability to produce sparks and shocks.¹² The Leyden jar allowed for transient storage of electric charge for the first time. It consisted of a glass jar lined with metal foil inside and out which accumulated equal and opposite electric charge on the respective metal surfaces

¹¹ See Purrington's discussion of the blurred line between dynamism and mechanism with reference to electromagnetic theory. For example, the Englishman James Clerk Maxwell, who attempted to mathematize electromagnetism in the 1860s, at times seemed to be a mechanist, at other times, a dynamist. Purrington, Robert D. "Nineteenth-Century Science in Context." In *Physics in the Nineteenth Century*, 9-31. New Brunswick: Rutgers University Press, 1999. See also, Caneva, Kenneth L. "Ampère, the Etherians, and the Oersted Connection." *The British Journal for the History of Science*, 13;2(1980):121-138 for a discussion of the French mathematician André-Marie Ampère's doubt about action-at-a-distance following Øersted's discovery.

¹⁰ Throughout, "molecules" refers to very small physical entities, not the current definition of molecule, which is defined as a group of atoms bonded together as a chemical compound. The mechanical, atomistic tradition is the Laplacian-Newtonian approach. Purrington, Robert D. "Nineteenth-Century Science in Context." In *Physics in the Nineteenth Century*, 9-31. New Brunswick, New Jersey: Rutgers University Press, 1999.

¹² Hunt, Bruce J. "Electricity: Currents and Networks." In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010.

when connected to a frictional generator of electricity via a metal rod.¹³ Its invention led to a spate of studies characterizing its effects.¹⁴

In 1791, the Italian medical professor Luigi Galvani (1737-1798) reported his observation that an electric spark near the exposed nerve of a dead frog leg led to a twitch—a brief muscle contraction.¹⁵ Upon further investigation, Galvani concluded that living things possess "animal electricity" that can be discharged through a conducting wire, similar to a Leyden jar. The Italian physicist Alessandro Volta (1745-1827) disagreed with Galvani's notion of animal electricity because of its affinity with the concept of the vital principle. According to Galvani, animal electricity helped explain the distinction between living beings and nonliving objects.¹⁶ Determined to prove the electricity Galvani observed in frog legs also can pass through inorganic materials, in 1800, Volta produced the electrical "pile": a stack of copper and zine disks separated by pieces of moist cardboard which could conduct electricity continuously. The pile, known soon after as the voltaic battery, produced sustained electrical currents and thus opened up new possibilities in the science of electricity. The Leyden jar could store current, but only briefly, while the voltaic pile's continuously re-charging current allowed experimenters to observe electricity's effects over a sustained period of time.¹⁷

¹³ Introduction of a conducting connection (e.g., a wire or a human hand) recombines the opposing charges. A Leyden jar is now understood as a capacitor because of its ability to store electric charge.

¹⁴ Hunt, Bruce J. "Electricity: Currents and Networks." In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010.

¹⁵ According to H. Bence Jones, "Du Bois-Reymond prefaces his own researches with an historical introduction, in which he goes back to Galvani's experiments." In 1852 Jones edited a translation of the abstract of Du Bois-Reymond's *Untersuchungen Über Thierische Elektricität*. The abstract included discussion of the first volume which appeared in 1848 and the first part of the second volume which appeared in 1849. The second part of the second volume did not appear until 1884. See Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, p 2. ¹⁶ Note the parallel between the notion of animal electricity and the vital principle.

¹⁷ Hunt, Bruce J. "Electricity: Currents and Networks." In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010; Purrington, Robert D. "Electromagnetism." In *Physics in the Nineteenth Century*, 32-74. New Brunswick: Rutgers University Press, 1999.

The 1819 discovery that electric currents produce magnetic forces, made by the Danish physicist Hans Christian Øersted (1777-1851), was perhaps the first insight that directed experimenters' attention to the force from current in Volta's battery. Øersted placed a magnetized compass needle near an electrified wire connected at each end to the poles of a battery and observed that the needle deflected away from the wire. The experiment proved conclusively that electric currents directly affect magnetized objects and represents the beginning of the study of electrodynamics.

Øersted had long believed in a dynamic interaction between electricity and magnetism. His education in Lutheran catechism and theology, which included a presentation of nature as the union of an infinite reason with an infinite divinely-imposed creative force, drew him to write a doctoral dissertation on Kant's dynamic philosophy of science.¹⁸ He was shaped heavily by the 1802 lectures on German Romanticism given by the philosopher Henrich Steffens (1773-1845) in Denmark and his acquaintance with the German idealist philosophers Johann Gottlieb Fichte (1762-1814) and Friedrich Wilhelm Joseph Schelling (1775-1854), and the German physicist Johann Wilhelm Ritter (1776-1810). His 1820 experiment was part of Schelling's *Naturphilosophie* (nature philosophy) quest to achieve a unified understanding of everything by elucidating the fundamental principles which explain all activity in nature. For Øersted and the *Naturphilosophen*, these fundamental principles were attractive and repulsive; they were opposing polar forces.¹⁹

¹⁸ For a discussion of the effect of Lutheran catechism and theology on Øersted's thought, see Wilson, Andrew D. "The Way from Nature to God." In *Hans Christian Ørsted and the Romantic Legacy in Science: Ideas, Disciplines, Practices.* Boston Studies in the Philosophy of Science, Vol. 241. Edited by Robert M. Brain, Robert S. Cohen, and Ole Knudsen, 1-11. Dordrecht, The Netherlands: Springer, 2007.

¹⁹ Newton's law of universal gravitation defines gravity as an attractive force (i.e., without polarity). Øersted's 1812 essay "View of the Chemical Laws of Nature Obtained Through Recent Discoveries" (1812) anticipates the unity of a "small number of interrelated, fundamental" principles which can explain all chemical phenomena; see p. 310 of the English-language collection of Øersted's work: Jelved, Karen, and Hans Christian Ørsted. *Selected Scientific Works of Hans Christian Orsted*. Edited by Andrew D. Jackson and Ole Knudsen. Princeton: Princeton University

Øersted and Ritter shared an interest in finding a broad connection between not only electricity and magnetism, but also between those two phenomena and chemistry, light and heat.²⁰ Ritter's investigation into chemical forces earned him the distinction, according to Øersted, as "the creator of modern chemistry."²¹ Ritter enrolled in the University of Jena in 1796, two years before Schelling arrived there. In 1797, Ritter read the experiments on galvanic activity in animals by German Romantic geographer and naturalist F. W. H. Alexander von Humboldt (1769-1859) and decided to undertake his own studies in galvanism—the electricity produced from chemical activity.²² Finding inspiration in Schelling's attempt, through *Naturphilosophie*, to establish a pan-organic natural science in response to Kant's limited knowledge of chemistry and to incorporate new revelations in electrochemistry deriving from the experiments of Galvani and Volta, Ritter saw his work as contributing to a vision of an

<sup>Press, 1998. For a discussion of Øersted's direct association with Fichte, Schelling, Steffens and Ritter see Möller,
P. L. "The Life of H. C. Oersted." In</sup> *The Soul in Nature, with Supplementary Contributions*. By Hans Christian
Oersted, translated by Leonora and Joanna B. Horner, vii-xxii. London: Dawsons of Pall Mall, 1966. See also, Hunt,
Bruce J. "Electricity: Currents and Networks" In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010; Purrington, Robert D.
"Electromagnetism." In *Physics in the Nineteenth Century*, 32-74. New Brunswick: Rutgers University Press, 1999.
For a comprehensive biography of Øersted, see Christensen, Dan Ch. *Hans Christian Ørsted: Reading Nature's Mind.* Oxford: Oxford University Press, 2013.

²⁰ Ritter's work in magnetochemistry was largely ignored after criticism from the respected German physicist Paul Erman in 1807. According to de Andrade Martins, the criticism "helped to bury magnetochemistry for several years, together with other results reported by Ritter." See de Andrade Martins, Roberto. "Ørsted, Ritter, and Magnetochemistry." In *Hans Christian Ørsted and the Romantic Legacy in Science: Ideas, Disciplines, Practices.* Boston Studies in the Philosophy of Science, Vol. 241. Edited by Robert M. Brain, Robert S. Cohen, and Ole Knudsen, 339-386. Dordrecht, The Netherlands: Springer, 2007, p. 345.

²¹ Jelved, Karen, and Hans Christian Ørsted. Selected Scientific Works of Hans Christian Orsted. Edited by Andrew D. Jackson, and Ole Knudsen. Princeton: Princeton University Press, 1998, p. 313. Wetzels says Ritter is "widely considered as the founder of electrochemistry." Wetzels, Walter D. "Johann Wilhelm Ritter: Romantic Physics in Germany." In Romanticism and the Sciences. Edited by Andrew Cunningham and Nicholas Jardine, 199-212. Cambridge: Cambridge University Press, 1990, p. 201. See also, Caneva, Kenneth L. "Ørsted's Presentation of Others' – and His Own – Work." In Hans Christian Ørsted and the Romantic Legacy in Science: Ideas, Disciplines, Practices. Boston Studies in the Philosophy of Science, Vol. 241. Edited by Robert M. Brain, Robert S. Cohen, and Ole Knudsen, 273-338. Dordrecht, The Netherlands: Springer, 2007; de Andrade Martins, Roberto. "Ørsted, Ritter, and Magnetochemistry." In Hans Christian Ørsted and the Romantic Legacy in Science: Ideas, Disciplines, Practices. Boston Studies in the Philosophy of Science, Vol. 241. Edited by Robert M. Brain, Robert S. Cohen, and Ole Knudsen, 339-386. Dordrecht, The Netherlands: Springer, 2007; de Andrade Martins, Robert S. Cohen, and Ole Knudsen, 339-386. Dordrecht, The Netherlands: Springer, 2007.

²² Wetzels, Walter D. "Johann Wilhelm Ritter: Romantic Physics in Germany." In *Romanticism and the Sciences*. Edited by Andrew Cunningham and Nicholas Jardine, 199-212. Cambridge: Cambridge University Press, 1990.

interconnected, living universe that placed galvanism as a unifying force.²³ According to du Bois-Reymond, Ritter and another German physicist Paul Erman (1764-1851) provided the first theory of muscular twitches. Ritter and Erman conceived of the nerve's transition to an altered state as responsible for conveying muscular movement in the form of twitches.²⁴

By the 1820s, the French physicist and mathematician André-Marie Ampère (1775-1836) found himself at odds with his contemporaries and countrymen. The majority of his scientific peers in France ignored or rejected Øersted's discovery and his corresponding idea of electromagnetic interaction. Ampère recognized their resistance stemmed from a belief in the two-fluid theory of magnetism promoted by the French engineer and physicist Charles-Augustin de Coulomb (1736-1806), who denied an interaction between electricity and magnetism. Ampère instead belonged to the group of etherians who, reminiscent of the *Naturphilosophen* in Germany, believed in the existence of an all-pervading ether which unified seemingly disparate physical phenomena.²⁵

As a result of his predilection toward uncovering a unifying causal explanation for natural phenomena in the ether and upon receiving word of Øersted's discovery, Ampère promptly embarked upon a series of experiments which showed that two electrified wires arranged in parallel attract or repel each other depending on if their current flows in the same or opposite direction. He went on to show that an electrified (i.e., current-carrying) wire coil behaves much like a magnet, appearing to manifest opposing poles. Ampère spent 1820 through 1827 developing the laws for the forces of electrodynamics by expressing them in mathematical

 ²³ Friedman, Michael. "Kant – Naturphilosophie - Electromagnetism." In *Hans Christian Ørsted and the Romantic Legacy in Science: Ideas, Disciplines, Practices*. Boston Studies in the Philosophy of Science, Vol. 241. Edited Robert M. Brain, Robert S. Cohen, and Ole Knudsen, 135-158. Dordrecht, The Netherlands: Springer, 2007.
 ²⁴ Du Bois-Reymond. *Untersuchungen über Thierische Elektricität*. Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1849, p. 386.

²⁵ Caneva, Kenneth L. "Ampère, the Etherians, and the Oersted Connexion." *The British Journal for the History of Science*, 13;2(1980):121-138.

form, and declared Coulomb's theories on distinct electric and magnetic fluids as incorrect. Ampère said, in contrast to Coulomb, that magnetism can be reduced to electricity and both phenomena depend on the same laws of forces. He theorized that magnetic force arises from the alignment of many small, molecular entities of electric current contained within magnets. These molecules, said Ampère, attract and repel each other through the ether.²⁶ Ampère's molecular vision of many polar units interacting to create force is very much like the theory du Bois-Reymond invoked when describing electromotive force in the nerves and muscles of frogs' legs.²⁷

A year after word of Øersted's discovery swept Western European and U.S. scientific circles, the English physicist Michael Faraday (1791-1867) confirmed the symmetric unification of electricity and magnetism; he showed an electric current-carrying wire can be made to rotate continuously around a magnetic pole. Faraday was opposed to the action-at-a-distance view of physics which dominated in France, and instead asserted that matter can be reduced to the dynamic interaction of forces pervading space. As a theorist as well as an experimentalist shaped by chemical ideas of polarity and his devotion to Sandemanian Christianity, Faraday, like Øersted, wrote about electricity and magnetism as reciprocally opposed forces working in unity. Faraday's devotion to Sandemanian Christianity reflected his commitment to understanding the symmetry and beauty of the universe, and of describing the physical world simply and directly, without invoking mathematical principles.²⁸

²⁶ Caneva, Kenneth L. "Ampère, the Etherians, and the Oersted Connexion." *The British Journal for the History of Science*, 13;2(1980):121-138; Hunt, Bruce J. "Electricity: Currents and Networks." In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010; Purrington, Robert D. "Electromagnetism." In *Physics in the Nineteenth Century*, 32-74. New Brunswick, New Jersey: Rutgers University Press, 1999.

 ²⁷ Du Bois-Reymond read and was familiar with Ampère's work. Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*. Cambridge, MA: The MIT Press, 2013, pp. 24, 64.
 ²⁸ See Cantor, Geoffrey. *Michael Faraday: Sandemanian and Scientist: A Study of Science and Religion in the Nineteenth Century*. London: MacMillan, 1991; Purrington, Robert D. "Electromagnetism." In *Physics in the*

Whereas Ampère's work engaged with steady currents, Faraday's observations of currents as they changed helped to elucidate as-yet-unknown electromagnetic interaction. In 1831, Faraday discovered electromagnetic induction with the aid of a galvanometer, a device for measuring electrical current developed the year of Øersted's discovery by the German chemist and physicist Johann Schweigger (1779-1857). Schweigger's galvanometer, which he named after Galvani, was a device which detected electric current and consisted essentially of a wire coil wrapped around a magnetic needle. Schweigger placed the coil around the needle to improve the device's sensitivity; more turns in the coil rendered the galvanometer a more sensitive a detector of electric current. In 1827, the Italian physiologist Leopoldo Nobili (1784-1835) applied the astatic galvanometer, which he developed two years earlier, to the measurement of current in the frog's limb. The astatic galvanometer removed from the recording device the disturbing effect of the earth's magnetic field. The device consisted of two magnetic needles mounted in parallel, with their poles reversed; only the needle closer to the ground would be affected by torque from the earth's magnetic field. According to du Bois-Reymond, Nobili was the first to apply the principles of electromagnetic action to demonstrate electric current in the frog. Nobili was also among the group of researchers who noted the directionality of current (i.e., the presence or intensity of muscular contraction depends on whether the current travels from the nerves proximally to distally, or in the reverse direction).²⁹ Neurophysiologists continued to use a galvanometer as the primary tool to detect electric current in nerves and muscles well into the twentieth century.

Nineteenth Century, 32-74. New Brunswick: Rutgers University Press, 1999; Hunt, Bruce J. "Electricity: Currents and Networks." In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010; Williams, L. Pearce. *Michael Faraday: A Biography*. New York: Basic Books, 1965.

²⁹ See Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852. See du Bois-Reymond, Emil. *Untersuchungen über thierische Elektricität*. Vol. 1 and Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1848 and 1849, pp. 66-69.

Faraday observed magnetic induction of electric currents while experimenting with suddenly starting or stopping the current in a wire coil wrapped around an iron ring. In a series of experiments he reported to the Royal Society on November 24, 1831, Faraday began by showing that a current passing through one wire induces a transient current in a parallel wire. When, and only when, he stopped the inducing current (from the voltaic battery) in the first wire, did he observe in the second wire another transient current of the same intensity, but in the opposite direction.³⁰ In a letter to his friend, the English chemist and druggist, Richard Phillips (1778-1851), Faraday concluded:

Electricity in currents therefore exerts an inductive action like ordinary electricity, but subject to peculiar laws. The effects are a current in the same direction when the induction is established; a reverse current when the induction ceases, and a *peculiar state* in the interim.³¹

Next, Faraday demonstrated the corresponding dynamic interaction between magnetism and electricity. He showed that bringing a wire coil connected to a galvanometer near the poles of a magnet caused a deflection in the device's needle. This was proof, he told Phillips, of "the evolution of *electricity from magnetism*." Like in "*volta-electric*" induction, in "*magneto-electric* induction":

> The currents were not permanent. They ceased the moment the wires ceased to approach the magnet, because the new and apparently quiescent state was assumed, just as in the

³⁰ Faraday, Michael. "First Series." In *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839, par. 6-26. See also Jones, H. Bence. "Life of Faraday – Chapter 1." *The Life and Letters of Faraday*. Vol. 2. Philadelphia: Lippincott, 1870, pp. 1-125.

³¹ Michael Faraday to R. Phillips, November 29, 1831, in *The Life and Letters of Faraday*. Vol. 2, by H. Bence Jones. Philadelphia: Lippincott, 1870, p. 7.

case of the induction of currents. But when the magnet was removed, and its induction therefore ceased, the return currents appeared as before.³²

Faraday described this "new electrical condition which intervenes by induction between the beginning and end of the inducing current" as the reason why previous attempts to reveal magnetic effects on chemical or electric action had failed—the induced currents were too short in duration and escaping detection.³³ He called the new electrical condition the "electrotonic state." Faraday considered this peculiar alteration from a previous state "as *equivalent* to a current of electricity."³⁴ The altered electrotonic state, furthermore, had to do with particles in the wire (or other conducting matter) acting toward a "*transference of elements*" to the poles of the voltaic pile used to induce the current.³⁵ In the electrotonic state, therefore, the "homogeneous particles of matter" align in "a regular but forced electrical arrangement in the direction of the current," and, upon relief of the inducting current, produce a return current in the opposite direction.³⁶

Faraday's appeal to particles in "a regular but forced electrical arrangement in the direction of current" as the mechanistic explanation of the electrotonic state is suggestive of Ampère's conception of magnetic force consisting of tiny polar molecules working through attraction and repulsion. Indeed, du Bois-Reymond would combine both concepts when attempting to explain the mechanism of electromotive force in nerves and muscles.

³² Michael Faraday to R. Phillips, November 29, 1831, in *The Life and Letters of Faraday*. Vol. 2, by H. Bence Jones. Philadelphia: Lippincott, 1870, p. 8. See also, Faraday, Michael. "First Series." In *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839, par. 27-59.

³³ Michael Faraday to R. Phillips, November 29, 1831, in *The Life and Letters of Faraday*. Vol. 2, by H. Bence Jones. Philadelphia: Lippincott, 1870, p. 8.

³⁴ Faraday, Michael. "First Series." In *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839, p. 19.

³⁵ Michael Faraday to R. Phillips, November 29, 1831, in *The Life and Letters of Faraday*. Vol. 2, by H. Bence Jones. Philadelphia: Lippincott, 1870, p. 8. See also, Faraday, Michael. "First Series." In *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839, par. 76, pp. 21-22.

³⁶ Faraday, Michael. "First Series." In *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839, par. 76, pp. 21-22.

In 1837, Faraday elaborated on his idea of a particular molecular arrangement of "contiguous particles" as necessary for current to move through a conducting substance. He discovered that chemical decomposition ensues by delivering electric current along wires contacting electrolytic liquids, but the effect did not occur with solids. Thus, Faraday arrived at his conception of the action and rearrangement of contiguous particles during induction through his experiments with electrolysis in liquids, declaring that induction occurs first (in both solids and liquids) and decomposition through electrolytic action happens next (in liquids only). Presented in opposition to action-at-a-distance theory, Faraday said the particles acted contiguously-from one neighbor to another-to create lines of electric force. These lines of force acted through a medium beyond the limit of physical bodies. Electromagnetic induction, therefore, arose by cutting through lines of force. In the opening paragraph of his "Eleventh Series," where he described his theory of contiguous particles, which he conceived of by working with electrolytic liquids, Faraday expounded on the need to combine analogy with experiment and his guess that perhaps every effect observable in inorganic and organic matter can be attributed to electricity, chemistry and magnetism, or the universal power in nature.³⁷ In 1841, Faraday demonstrated the effects of magnetism on light.³⁸

³⁷ "The science of electricity is in that state in which every part of it requires experimental investigation; not merely for the discovery of new effects, but what is just now of far more importance, the development of the means by which the old effects are produced, and the consequent more accurate determination of the first principles of action of the most extraordinary and universal power in nature:—and to those philosophers who pursue the inquiry zealously yet cautiously, combining experiment with analogy, suspicious of their preconceived notions, paying more respect to a fact than a theory, not too hasty to generalize, and above all things, willing at every step to cross examine their own opinions, both by reasoning and experiment, no branch of knowledge can afford so fine and ready a field for discovery as this. Such is most abundantly shown to be the case by the progress which electricity has made in the last thirty years: Chemistry and Magnetism have successively acknowledged its over-ruling influence; and it is probable that every effect depending upon the powers of inorganic matter, and perhaps most of those related to vegetable and animal life, will ultimately be found subordinate to it." Faraday, Michael. "Eleventh Series." In *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839.
³⁸ Today we understand light as the carrier of electromagnetic force. Faraday, Michael. "Nineteenth Series." In *Experimental Researches in Electricity*. Vol. 3. London: Bernard Quaritch, 1855.

Faraday articulated the antecedent to modern field theory; he imagined the space around magnets not as an inert void, but as teeming with activity. Soon after his work on electromagnetism, the Scottish mathematical physicist James Clerk Maxwell (1831-1879) and the British mathematical physicist and engineer William Thomson (1824-1907; who in 1892 received the title Lord Kelvin) began to mathematize Faraday's ideas.³⁹ Faraday's experimental research provided an exemplar for turning experimenters' and theorizers' attentions to the activity which transpires between objects, in addition to the changes in objects themselves.⁴⁰ Du Bois-Reymond's studies of the electromotive force in the frog nerve-muscle preparation thus brought out the epistemology that emerged out of nineteenth-century electrodynamics.

The philosophical foundation from Descartes to Kant

Kant's revolutionary dynamic philosophy significantly shaped German physics and the study of electrodynamics in the nineteenth century. Indeed, Kant's dynamical system of physics featured in prominent German textbooks of physics and served as the reference point from which German *Naturphilosophie* evolved.⁴¹ Emil du Bois-Reymond's physiological studies of the action current represent the "normal science" developing from galvanism and the new science of electromagnetism, but his work also must be understood as within a framework of looking at the

³⁹ See, e.g., Faraday, Michael. *Experimental Researches in Electricity*. Vol. 1. London: Bernard Quaritch, 1839 (there are three volumes of Faraday's communications appearing in the *Philosophical Transactions of the Royal Society*); Morus, Iwan Rhys. *Michael Faraday and the Electrical Century*. Cambridge: Icon Books, 2004; Purrington, Robert D. "Electromagnetism." In *Physics in the Nineteenth Century*, 32-74. New Brunswick: Rutgers University Press, 1999; Hunt, Bruce J. "Electricity: Currents and Networks." In *Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein*, 68-93. Baltimore: The Johns Hopkins University Press, 2010; Williams, L. Pearce. *Michael Faraday: A Biography*. New York: Basic Books, 1965.

⁴⁰ See e.g., Nersessian, Nancy J. *Faraday to Einstein: Constructing Meaning in Scientific Theories*. Dordrecht: Martinus Nijhoff Publishers, 1984.

⁴¹ Purrington, Robert D. "Nineteenth-Century Science in Context." In *Physics in the Nineteenth Century*, 9-31. New Brunswick: Rutgers University Press, 1999; Jungnickel, Christa and Russell McCormmach. "Establishing Physics at the Universities." In *The Second Physicist: On the History of Theoretical Physics in Germany*. Archimedes: New Studies in the History and Philosophy of Science and Technology, Vol. 48. Edited by Jed Z. Buchwald, 51-72. Switzerland: Springer, 2017.

natural world through the lens of emergence and development.⁴² This occurred across several disciplines in the nineteenth century, including philosophy, astronomy and cosmology, geology, and embryology and biology.⁴³

In the seventeenth century, the French philosopher René Descartes (1596-1650) espoused his mechanical philosophy that posited the cosmos and all its components are a geometricallyordered machine governed by mathematical principles. The fixed and unchanging laws of mathematics appealed to Descartes because they offered natural philosophers sure foundations for making sense of the world. The success of the Cartesian philosophy opened it up to criticism, however. Many were concerned with the status of human freedom and its place within a mechanical philosophy. The German philosopher Gottfried Wilhelm Leibniz (1646-1716) articulated a radical reconceptualization of Cartesian mechanisms towards the end of that century. Leibniz, in contrast to most mechanists of his time, conceived of animal and human bodies as automata with active agency. In his vision, dynamic machinery collaborate to bring about overall harmony in nature.

Leibniz rejected Descartes' claim that animals have no soul and asserted instead that *everything* has a soul. Intent on establishing a mechanistic account of a dynamic, preestablished harmony in nature, Leibniz rejected the static Cartesian notions of extended mass and motion,

⁴² In 1962, Thomas Kuhn presented his conception of the process of scientific knowledge production as passing through periods of "normal science" in which the majority of scientists participate in the puzzle-solving endeavors outlined by a central paradigm to revolutions in which new paradigms arise, redefining the expectations for problem-solving. Kuhn, Thomas. *The Structure of Scientific Revolutions*. Chicago: The University of Chicago Press, 1970. Gabriel Finkelstein argued that du Bois-Reymond's adherence to a materialist experimental physiology aligned with the normal science of contemporary biology which framed dynamic organic processes in terms of functions acting in space. Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*. Cambridge, MA: The MIT Press, 2013, pp. 29-75.

⁴³ Toulmin and Goodfield argued that a progressive, evolutionary conception of time reached across disciplines in the nineteenth century. Toulmin, Stephen, and June Goodfield. *The Discovery of Time*. New York: Harper & Row, 1965. Thomas Kuhn considered "normal science" as the regular work of scientists as they attempt to answer questions set out by the dominant scientific framework, or paradigm, of their time. Kuhn, Thomas S. *The Structure of Scientific Revolutions*. Chicago: The University of Chicago Press, 1970.

replacing them with perception and force, respectively. He placed perception and thought in matter itself, claiming that nature is unintelligible without a metaphysical principle underlying all material events. Naming perception as the primary substance, Leibniz said the cosmos could be reduced to individual perceptive souls—monads—which allow for activity arising from mechanism.⁴⁴ In addition, according to Leibniz, the Cartesian concept of motion simply explained relations between objects. Force, on the other hand, was a real entity which sprang from the *inside* of a material body. The *vis viva*, or "living force" was immaterial, active and self-organizing. Without it, contended Leibniz, nothing would happen.⁴⁵

Leibniz and Christian Wolff (1679-1754) were among the German philosophers concerned with the status of metaphysics at the end of the seventeenth century. The geometrical method of Cartesian physics and the inductive-mathematical method of Newton presented a serious challenge to the previously dominant Aristotelian metaphysics of scholastic forms and deductive syllogistic reasoning. Leibniz and Wolff tried to save metaphysics by introducing a mathematical method for rigorously deducing theorems from clearly defined terms.

The Leibnizian-Wolffian methodology faced resistance from opposing philosophers who insisted on empiricism and induction well into the 1750s, the beginning of Immanuel Kant's intellectual career. Leibniz's vision of a metaphysical, dynamic mechanism working to restore harmony after systemic change or imbalance helped shape Kant's formulation of transcendental knowledge.⁴⁶

 ⁴⁴ Riskin, Jessica. "The Passive Telescope or the Restless Clock." In *The Restless Clock: A History of the Centuries-Long Argument Over What Makes Living Things Tick*, 77-112. Chicago: The University of Chicago Press, 2016. See also, Jolley, Nicholas (ed.). *The Cambridge Companion to Leibniz*. Cambridge: Cambridge University Press, 1995.
 ⁴⁵ Jolley, Nicholas (ed.). *The Cambridge Companion to Leibniz*. Cambridge: Cambridge University Press, 1995, p. 310.

⁴⁶ Guyer, Paul. "Kant's Intellectual Development: 1746-1781." In *The Cambridge Companion to Kant*. Edited by Paul Guyer, 26-61. Cambridge: Cambridge University Press, 1992.

Looking for a universal principle to explain the origin of the cosmos, Kant introduced an evolutionary aspect to cosmology based on Newtonian forces in 1755.⁴⁷ Early matter was chaotic, he said, a random distribution of particles. Forces of attraction and repulsion turned the chaos into order by means of an "essential striving" toward organization and complexity. Kant's nebular hypothesis described the formation of planetary bodies as the result of gravity acting dynamically on matter—pushing and pulling with a purpose—over extended periods of time. According to Kant, cosmic self-organization is goal-directed toward perfection, and it evolves naturally over time, achieved through the active force of gravity.⁴⁸ By positing astronomical progress, Kant put purpose into dynamic material forces.

Kant's critical philosophy was a response to what he perceived as the pressing question of the day – how to reconcile the problem of human freedom with the mathematical worldview of Isaac Newton.⁴⁹ His transcendental idealism criticized conventional metaphysics for trying to derive concepts of understanding without corresponding evidence from sensibility, and proposed instead a union of rationality and empiricism as a way to reach the pure understanding. He reframed the long-held position that "all our knowledge must conform to the objects," flipping it

⁴⁷ Peter J. Bowler notes that Kant's 1755 Universal Natural History and Theory of the Heavens containing the nebular hypothesis was never issued and thus went largely unnoticed until Pierre-Simon Laplace discussed and elaborated on it in 1796. See Bowler, Peter J. Evolution: The History of an Idea. Third Edition. Berkeley: University of California Press, 2003, pp. 58-59. The Stanford Encyclopedia of Philosophy entry in Section "6. Systematic Cosmology: 'All Things in the Universe Interactively Connect" of Kant's Philosophical Development (revised Nov. 25, 2014), states that Universal Natural History publisher "Petersen went bankrupt just when copies of the Universal Natural History were off the press and in a warehouse. The warehouse was sealed—and then mysteriously burned down, which allowed Petersen to collect insurance and pay off creditors. Bankruptcy and fire prevented the book's distribution." Schönfeld, Martin, and Thompson, Michael, "Kant's Philosophical Development." In The Stanford Encyclopedia of Philosophy. Winter 2019 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/archives/win2019/entries/kant-development/.

⁴⁸ Toulmin, Stephen, and June Goodfield. "The Revival of Natural Philosophy." In *The Discovery of Time*, 74-102. New York: Harper & Row, 1965.

⁴⁹ Guyer, Paul. "Kant's Intellectual Development: 1746-1781." In *The Cambridge Companion to Kant*. Edited by Paul Guyer, 26-61. Cambridge: Cambridge University Press, 1992.

on its head by supposing instead that objects conform to knowledge originating in the subject.⁵⁰ From Kant's perspective, the self-conscious "I", through judgment, would point the way to pure all-comprehension of the norms of being.⁵¹

Kant declared his method a revolutionary break from conventional metaphysics. By positioning subjective knowledge as the starting point, Kant undertook a novel investigation of knowledge, asking not only how it is we come to understand, but also how understanding shapes our experience of, for example, a series of causally-related events occurring in temporal succession.⁵² Tied to his new epistemology, Kant attempted to create a new metaphysics of nature whose task was to determine the dynamics of nature by uncovering, through reasoning, "the inner forces of things, the first causes of the laws of motion and the ultimate constituents of matter."⁵³

Kant maintained that our certainty of physical laws derives from our own intuition. Because we have the intellectual capacity to impose physical laws from what we learn from nature via our senses, we must understand something about nature already. We choose to look at the world physically, said Kant, because of a universal understanding which unites our thoughts with all the objects of the universe. Kant established that we can actively produce universal and necessary knowledge which reflect the natural laws of the physical world using innate laws of

⁵¹ Kant began with an examination of how the "I" uses knowledge as an instrument to possess truth because, as his successor Georg Wilhelm Friedrich Hegel pointed out, "before we can get to the truth itself, we must first investigate the nature or type of the instrument in order to see whether it is capable of accomplishing what is required of it." Hegel, Georg Wilhelm Friedrich. "D. Recent Philosophy: Kant, Fichte, Jacobi, Schelling." In *Lectures on the History of Philosophy: The Lectures of 1825-26, Vol. III.* Edited by Robert F. Brown, translated by Robert F. Brown, J. M. Stewart and H. S. Harris. Berkeley: University of California Press, 1990, p. 218.
 ⁵² Engstrom, Stephen. "Knowledge and its object." In *Kant's Critique of Pure Reason: A Critical Guide.* Edited by James R. O'Shea, 28-45. Cambridge: Cambridge University Press, 2017. See also, Pinkard, Terry. *German Philosophy 1760-1860: The Legacy of Idealism.* Cambridge: Cambridge University Press, 2002.
 ⁵³ Guyer, Paul. "Kant's Intellectual Development: 1746-1781." In *The Cambridge Companion to Kant.* Edited by Paul Guyer, 26-61. Cambridge: Cambridge University Press, 1992, p. 31.

⁵⁰ Engstrom, Stephen. "Knowledge and its Object." In *Kant's Critique of Pure Reason: A Critical Guide*. Edited by James R. O'Shea, 28-45. Cambridge: Cambridge University Press, 2017, p. 29.

the mind.⁵⁴ With the goal of demonstrating the fundamental principles of science and morality as co-constituted by our thoughts and sense perceptions, just like the determination of objects and concepts relating in space and time, Kant began his project of grounding foundational principles for scientific knowledge to our experience.⁵⁵

Kant's conception of causality is integral to his endeavor to create a metaphysics grounded in experience. He attempted to account for the Scottish philosopher David Hume's skepticism that we could never achieve genuine objective knowledge of the world through our subjective exercise of reasoning by demonstrating that universal and necessary truths can be intellectually determined with the aid of sense perceptions—a process which involves a dynamic, interactive relationship between our sensibility and the noumenal world—the world as it is in itself, independent from human perception and experience. Hume doubted whether we could be certain about the relation between cause and effect because he conceived of an effect as a discrete event occurring at an instantaneous moment in time. Our conception of the order of time, said Hume, arises from the sequence of impressions and ideas which appear before the mind as matters of fact. Kant, in contrast, said we must have a robust metaphysical account of causality—of a necessary connection between cause and effect—because it makes possible an objective knowledge of temporal succession, which is independent of our subjective experience of successive representations appearing in consciousness.⁵⁶ Kant's dynamical theory of matter

⁵⁴ Guyer, Paul. "Introduction: The Starry Heavens and the Moral Law." In *The Cambridge Companion to Kant and Modern Philosophy*. Edited by Paul Guyer, 1-27. Cambridge: Cambridge University Press, 2006; Watkins, Eric. "Kant on the Distinction Between Sensibility and Understanding." In *Kant's Critique of Pure Reason: A Critical Guide*. Edited by James R. O'Shea, 9-27. Cambridge: Cambridge University Press, 2017.

⁵⁵ De Pierris, Graciela, and Michael Friedman. "Kant and Hume on Causality." In *The Stanford Encyclopedia of Philosophy*. Winter 2018 Edition. Edited by Edward N. Zalta,

https://plato.stanford.edu/archives/win2018/entries/kant-hume-causality/; Guyer, Paul. "Introduction: The Starry Heavens and the Moral Law." In *The Cambridge Companion to Kant and Modern Philosophy*. Edited by Paul Guyer, 1-27. Cambridge: Cambridge University Press, 2006.

⁵⁶ De Pierris, Graciela, and Michael Friedman. "Kant and Hume on Causality." In *The Stanford Encyclopedia of Philosophy*. Winter 2018 Edition. Edited by Edward N. Zalta,

allowed him to think of space and time not as objects, but as part of our intuitive process. He declared the perceived sequence of time as subjective, and considered causal events and mutual interactions between causally-linked substances as continuous changes of state over time which we can experience and transform into understanding with the aid of our sense perceptions.⁵⁷ Thus, Kant recognized a flow, a movement between subjectivity and objectivity. His dynamic conception of knowledge was revolutionary.

Kant's engagement with Hume's skepticism through the principle of causation brings to light his understanding of the dynamic temporal conditions of understanding and, consequently, of the natural order. Placing the concept of force within that of causality, Kant viewed causal relations between things as the activity of forces passing from one object to another. Kant was concerned with constructing the world not as a series of discrete events, but as explaining the world as a series of temporally determinate states of objects which passively receive their determinations from the causal power (i.e., active force) of other objects. Attending to the activities of objects and of ourselves, therefore, tells us something about their causes. To Kant, our being (i.e., our essence and existence) grounds (causes) our actions (effects). Considering human freedom the ultimate aim of nature, Kant articulated a law of final causes in order to account for free will; this notion of teleological causation depends on his insistence that both the causal laws of nature and the laws of reason guide our freely chosen actions.⁵⁸

https://plato.stanford.edu/archives/win2018/entries/kant-hume-causaliy/. See also Friedman, Michael. "Laws of Nature and Causal Necessity." *Kant-Studien*, 105(2014):531-553.

⁵⁷ Watkins, Eric. *Kant and the Metaphysics of Causality*, Cambridge: Cambridge University Press, 2005; Westphal, Kenneth R. "Kant's Dynamical Principles: The Analogies of Experience." In *Kant's Critique of Pure Reason: A Critical Guide*. Edited by James R. O'Shea, 184-204. Cambridge: Cambridge University Press, 2017; De Pierris, Graciela, and Michael Friedman. "Kant and Hume on Causality." In *The Stanford Encyclopedia of Philosophy*. Winter 2018 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/archives/win2018/entries/kant-hume-causality/<u>_</u>

⁵⁸ Watkins, Eric. Kant and the Metaphysics of Causality, Cambridge: Cambridge University Press, 2005.

At the turn of the nineteenth century, German idealist philosophers attempted to find a way out of the dualism Kant established between the faculties of understanding and sensibility. In Kant's formulation, a transcendental harmony unites the two faculties, but he could not explain how the two interacted with one another. Kant's insistence that we could know only the phenomenal world and not the noumenal world—things-in-themselves—was insufficient to some in the tradition of *Naturphilosophie*, leaving them with the epistemological imperative for overcoming his dualism.⁵⁹

Materialism and studies of the action current

In Germany, a dynamical physics emanating from the Kantian system which espoused the forces of active powers inherent in matter made its way into textbooks, and then the idealist *Naturphilosophie* of Schelling and his contemporaries shaped the work of the prominent physicists Øersted and Ritter.⁶⁰ To explain how the subject and object interact to form genuine objective knowledge through our experience, German idealists after Kant first accepted the idea of an absolute, single and infinite substance—a living, or "vital" force, pervading and linking everything. Recognition of the vital force drew from Kant's model of teleological progress outlined in the *Critique of Judgment*, which explained teleology in organic terms.⁶¹ Belief in a vital force corresponded with *Naturphilosophen* thinking of the absolute in organic, rather than mechanical terms. According to the German idealism scholar Frederick Beiser, an organic conception of the absolute agreed with the new sciences of electricity, magnetism, and biology which demanded a more dynamic view of matter. Furthermore, it allowed a view of the mind and

⁵⁹ Beiser, Frederick C. "Introduction: Hegel and the Problem of Metaphysics." In *The Cambridge Companion to Hegel*. Edited by Frederick C. Beiser, 1-24. Cambridge: Cambridge University Press, 1993.

⁶⁰ Purrington, Robert D. "Nineteenth-Century Science in Context." In *Physics in the Nineteenth Century*, 9-31. New Brunswick: Rutgers University Press, 1999.

⁶¹ Forster, Michael. "Hegel's Dialectical Method." In *The Cambridge Companion to Hegel*. Edited by Frederick C. Beiser, 130-170. Cambridge: Cambridge University Press, 1993.

body, or phenomenal and noumenal world, as different not in kind, but in degrees of organization and development of the living force, thus forging a path to address Kant's dualism.⁶²

Naturphilosophie faced opposition, however, and in 1847, four German physiologists— Emil du Bois-Reymond, Hermann van Helmholtz (1821-1894), Carl Ludwig (1816-1895), and Ernst Brücke (1819-1892)—all associated with Johannes Müller (1801-1858), an originator of experimental physiology and a vitalist, published their manifesto declaring that all biological life could be explained in physical and chemical terms. The manifesto was a direct attack on vitalism; the four physiologists argued there is no force or life spirit separate from physical and chemical forces of nature.⁶³

Scholars have placed materialism's rise as directly related to the European revolutions of 1848, as bourgeois classes wielded materialistic doctrines to deny the legitimacy of a divine right of kings.⁶⁴ As historian John Tresch has shown, however, mid-nineteenth-century materialism in France and Germany especially, must be understood as incorporating Romantic ideals of progress and order.⁶⁵ Although du Bois-Reymond was a fierce supporter of a mechanistic materialism to disprove Romantic vitalism, his worldview drew from earlier German Romantics like Humboldt and Johann Wolfgang von Goethe (1749-1832), and the German idealist *Naturphilosophie* tradition emanating from Kant and expressed by Schelling, Hegel, and Ritter which espoused the inherent orderliness of nature while appealing to rational change and

 ⁶² Beiser, Frederick C. "Introduction: Hegel and the Problem of Metaphysics." In *The Cambridge Companion to Hegel*. Edited by Frederick C. Beiser, 1-24. Cambridge: Cambridge University Press, 1993.
 ⁶³ Porter, Roy. *The Cambridge Illustrated History of Medicine*. Cambridge: Cambridge University Press, 2001, p.

^{179.}

⁶⁴ See, e.g., Temkin, Owsei. "Materialism in French and German Physiology in the Early Nineteenth Century." In *The Double Face of Janus and Other Essays in the History of Medicine*, 340-345. Baltimore: Johns Hopkins University Press, 2006; Tresch, John. *The Romantic Machine: Utopian Science and Technology after Napoleon*. Chicago: The University of Chicago Press, 2012.

⁶⁵ Tresch, John. *The Romantic Machine: Utopian Science and Technology After Napoleon*. Chicago: The University of Chicago Press, 2012.

adaptation.⁶⁶ Indeed, in an 1849 letter to Ludwig, du Bois-Reymond declared, "[e]very industrious and ambitious man of science...is Humboldt's son; we are all his family."⁶⁷ Humboldt, a figure "between Enlightenment and Romanticism," observed the electromotive force in experiments performed at the end of the eighteenth century, but maintained that the vital force could not be reduced to any single force or material substance.⁶⁸

Humboldt was an early supporter of Schelling's *Naturphilosophie* as it was consistent with his belief in an exploration of nature in order to understand the development of the self. Schelling, for his part, drew from Humboldt's work on electrophysiology when crafting one of his major works on *Naturphilosophie*. Humboldt, like Schelling, believed in the interconnectedness of nature, but later became wary of Schelling's disciples in the face of criticism decrying speculative philosophy as a hinderance and distraction from inductive, experimental science.⁶⁹

In response to the French Revolution, Schelling engaged in a project linking human freedom to aesthetic beauty.⁷⁰ Schelling's *Naturphilosophie* celebrated an inner freedom, positing that nature itself is striving toward its absolute inner freedom, acting through its own

⁶⁶ Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013. See also, Cranefield, Paul F. "Carl Ludwig and Emil du Bois-Reymond - A Study in Contrasts." *Gesnerus: Swiss Journal of the History of Medicine and Sciences*, 45(1988):271-282, p. 277: "His [du Bois-Reymond's] famous and often sarcastic essay on the *Lebenskraft* [vital force] was part of the preface to his 1848 book [*Investigations of Animal Electricity*], complete with its famous assertion that, in principle, analytical mechanics can reach even to the problem of "Freedom of the Will." See also Cunningham, Andrew and Nicolas Jardine (eds.). *Romanticism and the Sciences*. Cambridge: Cambridge University Press, 1990.

⁶⁷ Quoted in Finkelstein, Gabriel. "Conquerors of the Künlün"? The Schlagintweit Mission to High Asia, 1854-1857." *History of Science*, 38(2000):179-218, p. 179.

⁶⁸ Dettelbach, Michael. "Alexander von Humboldt Between Enlightenment and Romanticism." *Northeastern Naturalist*, 8;1(2001):9-20.

⁶⁹ Richards, Robert J. "Schelling: The Poetry of Nature." In *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*. Chicago: The University of Chicago Press, 2002, pp. 114-192.

⁷⁰ For discussions of the confluence of Idealism, Romantic aesthetics, and Schelling's *Naturphilosophie* see Beiser, Frederick C. *German Idealism: The Struggle Against Subjectivism, 1781–1801.* Cambridge, MA: Harvard University Press, 2002; Richards, Robert J. *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe.* Chicago: The University of Chicago Press, 2002; Zammito, John. "Reconstructing German Idealism and Romanticism: Historicism and Presentism." *Modern Intellectual History*, 1;3(2004):427-438.

sort of intelligence. This intelligence acts through a universal force common to all the cosmos; it is a polar force, said Schelling, a unity of opposites – attraction and repulsion – which directs nature's teleological progression toward absolute freedom.⁷¹

Hegel's philosophy helps to illuminate the post-Kantian German idealist presentation of a universe in development, progressively emerging into itself over time through dynamic interaction between objects and our subjective experience. Hegel was recruited to the Lutheran University of Jena by his friend Schelling in 1801. They had been roommates and close friends during their philosophical and theological education at the Tübinger Stift. Although they became opponents by the end of the first decade of that century, their philosophical beliefs aligned closely, and Hegel drew from Schelling's philosophy when developing his own dialectical framework designed to show the possibility of knowledge beyond our own experience.⁷² By asserting a progressive march toward the absolute, Hegel articulated a teleological conception of knowledge.⁷³

⁷¹ Richards, Robert J. "Schelling: The Poetry of Nature." In *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*. Chicago: The University of Chicago Press, 2002, pp. 114-192; Morgan, S. R. "Schelling and the Origins of his *Naturphilosophie.*" In *Romanticism and the Sciences*. Edited by Andrew Cunningham and Nicholas Jardine, 25-37. Cambridge: Cambridge University Press, 1990; Wetzels, Walter D. "Johann Wilhelm Ritter: Romantic Physics in Germany." In *Romanticism and the Sciences*. Edited by Andrew Cunningham and Nicholas Jardine, 199-212. Cambridge: Cambridge University Press, 1990.

⁷² In his 1797 first major work of *Naturphilosophie*, Schelling could consider the abstract "relationships among the infinite self, the absolute self's intuition, the empirical self, and nature as if they were formed with atemporal logical swiftness. He would portray the outcome of these creative logical-metaphysical relationships as the products of a self ever striving for reflexive comprehension, a self in the process of infinite becoming…however, one could turn the page and find Schelling mentioning the historical dimensions of the relationships that had initially been depicted in abstract terms. He would suggest that the actions of the ego played themselves out, stage after stage, in a larger temporal sphere, through the developmental history of mankind, from the period before the Greeks introduced reflective thought to his own age of critical philosophy. These historical stages would recapitulate in time the reproductive activities of the critical mind in search of itself." Richards, Robert J. "Schelling: The Poetry of Nature." In *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*, 114-192. Chicago: The University of Chicago Press, 2002, p. 135.

⁷³ Hegel showed how his dialectical logic determines concepts sequentially, each concept determined by earlier concepts through a three-stage process. The dialectical logic is an historical process which leads to the progressive determination of successive concepts from its predecessors. Hegel envisioned his logic as driving to increasingly comprehensive and universal knowledge which would eventually lead to complete knowledge, the absolute. Maybee, Julie E., "Hegel's Dialectics." In *The Stanford Encyclopedia of Philosophy*. Winter 2016 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/entries/hegel-dialectics; Beiser, Frederick C. "Introduction: Hegel and

Schelling's theory of everything, expressed in his *Naturphilosophie*, and Hegel's dialectic of emergence helped make possible physical studies in electrodynamics and, consequently, du Bois-Reymond's conceptualization of the nerve's action current as an altered state, moving through time to effect muscular contraction. Making use of recent discoveries in electromagnetism, which arose amidst a search for a unification of natural forces, du Bois-Reymond manipulated the temporal dynamics of current flow in frog nerve-muscle preparations in order to understand the relationship between electromotive force in nerves and muscles.

Despite his outspoken loyalty to the doctrine of mechanistic materialism for explaining life processes, du Bois-Reymond appreciated that physiologists made sense of observations through interpretation. His biographer Gabriel Finkelstein highlighted the physiologist's interest in theory as evidenced by his studies in comparative anatomy and embryology.⁷⁴ From du Bois-Reymond's perspective, however, "[e]mbryology still adhered to the Romantic concept of forms in time, whereas physiology preferred the more modern perspective of functions in space."⁷⁵

Du Bois-Reymond's move from descriptive to experimental work was situated within a mid-nineteenth-century shift in thinking about time on a biological scale. Considering functions in space allowed physiologists like du Bois-Reymond to posit that real entities, which move,

the Problem of Metaphysics." In *The Cambridge Companion to Hegel*. Edited by Frederick C. Beiser, 1-24. Cambridge: Cambridge University Press, 1993.

 ⁷⁴ Finkelstein, Gabriel. "Science." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*. Cambridge, MA: The MIT Press, 2013, pp. 57-76. Owsei Temkin argued the rise of the field of embryology in early nineteenth-century Germany can be linked directly to physiologists incorporating philosophy of history into "a concept of life in which each stage has its definite place." At the time, the historical point of view in German embryology assumed a continuity of bodily organization between animal species, with organisms alive at a particular moment in history representing a particular stage of development of the species, which progresses and adapts over time. See Temkin, Owsei. "German Concepts of Ontogeny and History around 1800." In *The Double Face of Janus and Other Essays in the History of Medicine*. Baltimore: The Johns Hopkins University Press, 2006 [1977], pp. 373-389, p. 374. Janina Wellmann argues the study of embryology helped incorporate the study of rhythms into biological inquiry. Rhythm became a means of organizing time. See Wellmann, Janina. *The Form of Becoming: Embryology and the Epistemology of Rhythm, 1760-1830*. Cambridge, MA: The MIT Press, 2017.
 ⁷⁵ Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*. Cambridge, MA: The MIT Press, 2013, p. 59.

interact, and change over time, accounting for all activity of physiological processes, can be reduced to physical principles. His studies of the action current represent the combination of continued interest in galvanism and the emerging theory of electromagnetism, which assumed the presence of real forces dynamically interacting through space and time.

In 1841, at the request of his teacher Müller, du Bois-Reymond began experiments to confirm and build upon results from Italian physiologist Carlo Matteucci's (1811-1868) experiments "On the Electrical Phenomena of Animals." He approached the problem with an understanding of both physics and physiology, and with a mechanistic hypothesis: that electricity drives action in nerves.⁷⁶ Du Bois-Reymond was not alone amongst his contemporaries in considering physiological change over time; with the aid of instrumentation, Wunderlich measured body temperature changes, Ludwig assessed blood pressure and flow, and Helmholtz determined the time course of nerve conduction and muscle contraction.⁷⁷

For his experiments, du Bois-Reymond used a galvanometer to detect flow of charge in nerve and muscle tissue of various animal species, but predominantly the frog.⁷⁸ The magnetic needle of the galvanometer pivoted as electric current passed through a copper wire coil attached to metal electrodes touching the animal tissue, which was the source of current.⁷⁹ According to

⁷⁶ Finkelstein, Gabriel. "Science." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013, pp. 57-76.

⁷⁷ Finkelstein, Gabriel. "Conquerors of The Künlün"? The Schlagintweit Mission to High Asia, 1854-57." *History of Science*. 38 (2000): 179-218, p. 184.

⁷⁸ The tradition of using frog legs to study "animal electricity" stems back to 1780 with the Italian physician and physicist Luigi Galvani. In his studies du Bois-Reymond used the rheoscopic limb preparation, modified from Galvani's rheoscopic frog, to observe muscular contractions without metallic intervention in a closed circuit. The rheoscopic limb consisted of a frog's leg and foot with the entire length of the sciatic nerve, from knee to loin, still attached. See Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852.

⁷⁹ Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852. Jones dedicated the English translation of Johannes Müller's German abstract of du Bois-Reymond's work on animal electricity to Faraday, assuring the Fullerian Professor of Chemistry in The Royal Institution (of Great Britain) "that the discoverer himself desires above all things to follow the example which you have set before him in his search after truth." According to Jones, both he and Faraday witnessed du Bois-Reymond perform his experiments at the Royal Institution. In the Preface,

Finkelstein, he chose the galvanometer by design: he wanted to show a physical device could detect electric charge in both organic and inorganic matter; he wanted to show "the equivalence of nervous and electrical current."⁸⁰

As mentioned above, Øersted's discovery of electricity's effect on magnetism led to the rapid development of the galvanometer as a tool to measure electromagnetic effects. Indeed, Faraday used the galvanometer consistently since the beginning of his studies on electromagnetism in 1821. The device also became indispensable to neurophysiological experiments well into the twentieth century. Du Bois-Reymond's experiments on electromotive force reveal the dependent relationship of neurophysiology research on devices, both material and analytical, for observing the nervous system and analyzing its function. This symbiotic relationship resulted in the devices themselves significantly shaping neuroscientific understanding and ways of representing scientific knowledge, as new measurement devices have done for other disciplines. In the 1830s, for example, the English mathematician and engineer Charles Babbage used a new device, the pyrometer, to obtain exact measurements of materials' expansion under the influence of heat. He combined new experimental data with help from mathematical calculations and his computing machine to support his belief in a geological theory of uniformitarianism-that a few fundamental principles give rise to varied geological phenomena. The diagrams and tables that Babbage and his tools produced helped replace the discipline's reliance on human testimony and ushered in a new way of thinking about geological change. Soon, measurements of heat helped to support uniformitarian theories. Furthermore,

Jones said, "as those who have witnessed Dr. du Bois-Reymond's experiments during his stay in England generally asked where they could find an account of what they had seen, I have the more readily used the opportunity which I possessed for obtaining the best information from him on all the points mentioned in the abstract. Many other and most interesting questions have been discussed, and hence some experiments and statements have been added to the German abstract," p. viii.

⁸⁰ Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013, p. 63.

Babbage's tools showed "geology was more than a collection of facts; it was a method that involved experimentation and particular concerns over accurate representation in science."⁸¹ Similarly, du Bois-Reymond's work illustrates how neurophysiology research was made possible through the development of new devices for experimentation and analysis.

In May 1842, du Bois-Reymond obtained results for his "Preliminary Abstract." Drawing heavily from physical principles, his work recognized the presence of electric current in all animals, and explained conduction in nerve and muscle in terms of flow of charge between different parts of the tissue. Consulting existing morphological muscle diagrams, he conceived of electric flow in muscles as within a closed-circuit cylindrical battery. The tissue surface represented the positive pole and the tissue center the negative pole, with the two poles participating in electric antagonism.⁸²

Du Bois-Reymond's physical account of electromotive force (i.e., the movement of electric current along a muscle or nerve) rested on the idea that peripolar molecules present in nerves and muscles rearrange themselves to produce electric current. In their 1871 first edition of *A Practical Treatise on the Medical and Surgical Uses of Electricity*, U.S. neurologists George Miller Beard and A. D. Rockwell likened the German physiologist's "molecular theory of animal electricity" to that of French physicist Charles-Augustin de Coulomb's two-fluid theory of magnetism, in which molecules of the same fluid repelled each other and attracted the molecules

⁸¹ Dolan, Brian. "Representing Novelty: Charles Babbage, Charles Lyell, and Experiments in Early Victorian Geology." *History of Science*, 36;3(1998):299-327, p. 315.

⁸² Finkelstein, Gabriel. "Science." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*, 57-76. Cambridge, MA: The MIT Press, 2013; Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, p. 95. Ritter had shown the galvanic current in organic and inorganic matter in 1798 but could not conclude whether galvanic action was linked to electricity, a chemical reaction, or had something to do with the fluid in nerves. He interpreted this finding as evidence for Schelling's *Naturphilosophie* project to prove unity between all matter. See Wetzels, Walter D. "Johann Wilhelm Ritter: Romantic Physics in Germany." In *Romanticism and the Sciences*. Edited by Andrew Cunningham and Nicholas Jardine, 199-212. Cambridge: Cambridge University Press, 1990.

of the other fluid.⁸³ Du Bois-Reymond's theory, however, ultimately did not resort to a theory of two fluids; rather, it aligned more closely with Ampère's theory and Faraday's conception of contiguous particles.

According to du Bois-Reymond, each individual molecule had polar zones—negative and positive. He accounted for his laws of muscle and nerve current by claiming a peripolar distribution of charge in the smallest sections of muscle and nerve [see **Figure 1.1**]. He was unable to explain, however, how the peripolar molecules rearranged themselves to become electromotive.⁸⁴ Electrophysiologists searched for analogous explanations well into the twentieth century.

⁸³ Beard, George M. and A. D. Rockwell, "Electro-Physiology – Animal Electricity." In *A Practical Treatise on the Medical and Surgical Uses of Electricity Including Localized and General Electrization*. New York: William Wood & Co., 1871, p. 51. In the footnote on page 48, Beard and Rockwell refer readers to Morgan, C. E. *Electro-Physiology and Therapeutics; Being a Study of the Electrical and Other Physical Phenomena of the Muscular and Other Systems During Health and Disease, Including the Phenomena of the Electrical Fishes*. New York: William Wood & Co., 1868 "for a more detailed and exhaustive explanation of the laws of the muscular and nerve currents." Morgan's book is dedicated to du Bois-Reymond. See also, Cranefield, Paul F. "Charles E. Morgan's 'Electro-Physiology and Therapeutics': An Unknown English Version of Du Bois-Reymond's 'Thierische Elektricität'. *Bulletin of the History of Medicine*, 31;2(1957):172-181. According to Cranefield, Morgan's book is essentially a translation of du Bois-Reymond's seminal 1848 and 1849 work *Untersuchungen über Thierische Elektricität*. Morgan worked in the laboratory of du Bois-Reymond from 1857-1864, and "was perhaps the first American physiologist to study in Berlin rather than Paris and perhaps the only American physiologist to come under the sway of the physical school at the peak of its self-confident, mechanistic ambitions," p. 176.

⁸⁴ Finkelstein, Gabriel. "Science." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*, 57-76. Cambridge, MA: The MIT Press, 2013.

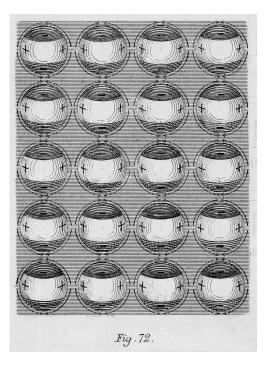


Figure 1.1: Du Bois-Reymond's diagram of the peripolar distribution of molecules in muscle. Courtesy of Gabriel Finkelstein.⁸⁵

For du Bois-Reymond, and for Matteucci—whose work was communicated by Faraday in June, 1845 to the Royal Society of London—understanding the animal preparation as an electromotor which generates electric current meant considering it as part of a circuit, around which current flows.⁸⁶ Based on Volta and Nobili's observations of tetanus (i.e., sustained muscular contraction) following delivery of rapidly-occurring sequential discharges of electric current generated from a battery to frogs' limbs, du Bois-Reymond postulated electric excitation in motor nerves as directly related to change in current over time.⁸⁷ He stated that motor nerves

 ⁸⁵ From du Bois-Reymond, Emil. Untersuchungen über thierische Elektricität. Vol. 1. Berlin: Verlag von G. Reimer, 1848 (Plate VI, Figure 72). Reprinted from Finkelstein, Gabriel. "Science." In *Emil du Bois-Reymond:* Neuroscience, Self, and Society in Nineteenth-Century Germany. Cambridge, MA: The MIT Press, 2013, p. 71.
 ⁸⁶ See, e.g., Matteucci, Carlo "Electro-Physiological Researches – First Memoir. The Muscular Current." Philosophical Transactions of the Royal Society of London. Part I. Communicated by Michael Faraday, 283-296. London: Richard and John E. Taylor, 1845; Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond. London: Churchill, 1852.
 ⁸⁷ Du Bois-Reymond said current change over time was more important than total current density: "By density of the current in any section of the circuit du Bois-Reymond expresses the quotient of the intensity of the current

get excited by variations of current "from one instant to another, and the excitation caused by these changes is the greater the more rapidly the changes take place, or the greater they are in any given time."⁸⁸

For his experiments on muscular and nervous currents, du Bois-Reymond induced tetanus as a way to amplify physiological time.⁸⁹ According to him, the problem with the frog rheoscopic preparation used first by Galvani and later by others, including Matteucci, was that observed muscular contraction occurred briefly, only when a circuit was made or broken. As a consequence, similar to the transient currents Faraday observed in his studies of electromagnetic induction, the experimenter could not get a sense of whether a permanent current or momentary discharge excited the nerve. Furthermore, the galvanometer was not sensitive enough to detect transient currents. Interested not only in the presence of the muscle and nerve currents, but also in their temporal and polar dynamics, du Bois-Reymond made use of the fact that the galvanometer's needle remained deflected during the sustained current of tetanus. By using tetanus to manipulate physiological time, du Bois-Reymond attempted to better understand the dynamic nature of the muscle and nerve currents.⁹⁰

divided by the size of the surface of the section of the conductor." Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, p. 58.

⁸⁸ Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, p. 58

⁸⁹ Finkelstein, Gabriel. "Science." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013, pp. 57-76. Du Bois-Reymond mentioned the frog writhing in pain. On p. 73, Finkelstein explains, "As du Bois-Reymond proved with the rheoscopic frog, the tetanic state actually consisted of a series of short muscular contractions. Each of these gave rise to a weak shock, but since they followed in rapid succession, the galvanometer summed their effects. In this way tetanus allowed investigators to match the transitory action of tissues to the extended reaction of instruments. Long before amplifiers and oscilloscopes, tetanus magnified physiological time."

⁹⁰ See, e.g., in Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. "Chapter VII: On the General Law of the Excitation of Nerves by an Electrical Current." In *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, pp. 58-65; Finkelstein, Gabriel. "Experiments." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany*. Cambridge, MA: The MIT Press, 2013, pp. 57-116.

Matteucci offered differing, sometimes conflicting accounts over several years about the nature of the muscular current during tetanus. Matteucci observed "induced contractions" in a secondary muscle making physical contact with the nerve connected to a primary tetanized muscle, and du Bois-Reymond attempted to prove that this resulted from electric current passing through the nerve to the secondary muscle. To do so, he devised an experiment in which the galvanometer would detect current in the secondary muscle during tetanus in the primary muscle. The device's needle deflected briefly in the negative direction upon application of external current causing tetanus in the primary muscle. To du Bois-Reymond, this "negative variation" of current (i.e., marked diminution or reversal from one instant to another) proved that electric signals passing through nerves causes contraction in muscles.⁹¹ According to H. Bence Jones, his English-language translator, "[b]y these experiments the true origin of the secondary contractions is placed beyond all doubt. They arise in consequence of those variations of the density of the muscular current in the nerve."92 Du Bois-Reymond's experiments showed current variation (over time) mattered for producing physiological action, not simply overall intensity. Furthermore, although the secondary contraction appeared to the naked eye as a sustained contraction (like that of tetanus), du Bois-Reymond used his modified frog rheoscopic limb to observe that the secondary contraction actually "consists of a series of rapidly following single contractions, each of which is accompanied by an equal fall and rise of the intensity of the

⁹¹ Finkelstein describes this observation as proof that electricity acts as a biological signal. Finkelstein, Gabriel. "Experiments." In *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013, p 72. See also, Finkelstein, Gabriel. "M. du Bois-Reymond Goes to Paris." *The British Journal for the History of Science*, 36;3(2003):261-300; Lenoir, Timothy. "Models and Instruments in the Development of Electrophysiology, 1845-1912." *Historical Studies in the Physical and Biological Sciences*, 17;1(1986):1-54.

⁹² Of note, H. Bence Jones published the two-volume work, *The Life and Letters of Faraday*. Philadelphia: Lippincott, 1870. Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, pp. 127-149, 144.

muscular current."⁹³ The oscillations of the "muscular current" in the nerve du Bois-Reymond observed during tetanus would soon be named the action current.⁹⁴ These experiments show clearly the importance of timing of electric current for producing physiological action in nerves and muscles.

Du Bois-Reymond also attempted to understand what happens in nerves while they cause contraction in muscles. According to Jones, du Bois-Reymond constructed experiments:

to investigate how the nervous current is affected while the nerve is conveying to the muscle, or to the central organs, those material changes which become perceptible as sensation and motion. For this purpose, some method must be found for putting the nerve into a state analogous to tetanus in the muscle.⁹⁵

Du Bois-Reymond also amplified physiological time in nerves to parallel what he did with tetanus in muscles. Borrowing from Faraday's concept of the electrotonic state, du Bois-Reymond introduced a permanent external "exciting current" to one portion of a frog's nerve and observed its effects on nearby portions. The excited portion of nerve acted as the battery. Du Bois-Reymond observed the movements of two galvanometers' needles from two portions of the nerve on either side of the battery: the two needles deflected in opposite directions. To du Bois-Reymond this was evidence that "a new electromotive action takes place in every point of the

⁹³ Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond. London: Churchill, 1852, pp. 127-149, 147; Finkelstein, Gabriel.
"Experiments." In Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany. Cambridge, MA: The MIT Press, 2013, pp. 57-116.

⁹⁴ In 2020, at the time of writing, it is called the action potential.

⁹⁵ Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, p. 174.

nerve, which has the same direction as the exciting current itself."⁹⁶ In other words, the nervous current is active and changing; it moves.

Du Bois-Reymond, like Matteucci, understood animal electricity as very likely depending on a chemical reaction or molecular rearrangement in the body of the organism.⁹⁷ Faraday's work on electromagnetic induction and electrolysis provided a direct analogy to electromotive action in nerve and muscle. Faraday knew their work—he observed du Bois-Reymond's experiments at the Royal Institution—and they certainly knew his work revealing electromagnetic induction and electrolysis from the 1830s. Jones pointed out that du Bois-Reymond borrowed Faraday's concept of the electrotonic state because it alluded to change from a previous state. "If the comparison between the induction of currents in wires and the irritation of the nerves is to be fully carried out," said Jones, "it is clear that the permanent arrangement of the electromotive molecules produced by the current in the nerves would correspond with Faraday's electrotonic state of matter.⁹⁸

Faraday's concept of molecular change as a result of magnetic influence shaped du Bois-Reymond's belief that the electromotive force passing through nerve and muscle represented a change from one state to another. Ritter, the German chemist and physicist inspired by Schelling's *Naturphilosophie* and Erman (another German physicist), opined on an altered state of the nerve as responsible for making muscles twitch. In *Untersuchungen über Thierische*

 ⁹⁶ Emphasis removed. Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond. London: Churchill, 1852, pp. 164-189, 180.
 ⁹⁷ Matteucci, Carlo "Electro-Physiological Researches – First Memoir. The Muscular Current." Philosophical Transactions of the Royal Society of London. Part I. Communicated by Michael Faraday, 283-296. London: Richard and John E. Taylor, 1845; Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. "Chapter XXV: On the Electrotonic State of the Nerves." In On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond, London: Churchill, 1852, pp. 174-186.

⁹⁸ Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852, pp. 185-186. See also, Finkelstein, Gabriel. "M. du Bois-Reymond Goes to Paris." *British Society for the History of Science*, 36:3(2003):261-300.

Elektricität (Investigations on Animal Electricity), du Bois-Reymond said of Ritter and Erman's theory of twitches:

As soon as with RITTER and P. ERMAN the first fundamentals of a theory of twitches appeared, the following conception appeared, that has gained importance with the approaches of NOBILI'S and to some extent BECQUEREL'S und MATTEUCCI'S: the conception that, the movement conveying process, that appears at the moment when the circuit is closed, is caused by a transition of the nerve to a different state: that the function of the current is to transplant the nerve into a different state and hold it there as long as itself (the current) continues; that the opening twitch is nothing other than an effect of the return of the nerve from the changed, back to its original state once the pressure of the stimulating current abides. Thus, RITTER'S vigorous remark, «the organism issues itself the opening beat».⁹⁹

Recent revelations in electromagnetism provided du Bois-Reymond with a way to

combine the concepts of electrotonus with electrolysis to explain the nerve's altered state.

Erman, according to du Bois-Reymond, speculated about the nature of the nerve's altered state,

imagining it as chemical "oxidation and hydrogenation" occurring in two zones of the nerve.¹⁰⁰

Du Bois-Reymond also mentioned a different conceptualization of the nerve's altered state

⁹⁹ The original German reads: "Sobald nämlich bei RITTER und P. ERMAN die ersten Grundzüge einer Theorie der Zuckungen auftauchten, machte sich auch folgende Vorstellungsweise geltend, die durch die ferneren Betrachtungen NOBILI'S, weniger BECQUEREL'S und MATTEUCCI'S, noch an Gehalt gewann: dafs nämlich der Bewegung vermittelnde Vorgang, der im Augenblick des Schliefsens der Kette entstehe, herrühre von dem Uebergange des Nerven in einen veränderten Zustand; dafs die Thätigkeit des Stromes eben darin bestehe, den Nerven in diesen veränderten Zustand zu versetzen und, so lange er selber andauere, auch darin zu erhalten; dafs endlich die Oeffnungszuckung nichts sei, als die Folge des Rücktrittes des Nerven aus dem veränderten Zustand in den natürlichen, sobald der Zwang des erregenden Stromes ein Ende habe. Daher RITTER'S markiger Ausdruck, «der Organismus ertheile sich den Oeffnungsschlag selbst»." Du Bois-Reymond. *Untersuchungen über Thierische Elektricität*. Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1849, p. 386.

¹⁰⁰ The original German reads: "gedenken wir nur in Kurzem, wie P. ERMAN, dem von seinen Versuchen an der unvollkommen geschlossenen Säule her das Bild des in zwei verschiedenartige Zonen zerfällten feuchten Leiters vorschwebte (S. oben Bd. I. S. 432), sich eine vorwaltende Oxydation und Hydrogenisation der einen und der anderen Nervenhälfte als das Wesentliche dabei dachte." Du Bois-Reymond. *Untersuchungen über Thierische Elektricität*. Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1849, p. 386.

presented by Nobili, who "differentiated the alteration occurring with decreasing and increasing current as «Alterazione diretta» and «Alterazione inversa»…while smartly avoiding proposing an opinion about said alteration of the matter."¹⁰¹ Du Bois-Reymond thought, in other words, that Erman's assumption about the mechanism behind the nerve's altered state was based on little to no evidence. Du Bois-Reymond admired Nobili, who also had no evidence to support a mechanistic claim, for resisting the urge to speculate.

Du Bois-Reymond interpreted the results of his experiments as contributing to the causal explanation of the nerve's action current as altered state. Erman's theory was not far off from the truth, he said, but his own work supported that the nerve action current maintained directionality. Through his theory du Bois-Reymond sought to extend Nobili's concept while giving credit to Erman's thoughts about chemical change in the nerve. His theory drew heavily from Faraday's work on the dynamic interactions of electricity, magnetism, and chemistry:

We have been able to recognize the persisting change in the nerves during the electrotonic state, caused by the electrical flow, that RITTER, ERMAN and NOBILI could only assume. If electricity meets a nerve, the latter responds as any other moist conductor. Electrolysis is achieved, which begins with columnar polarization. The transition from normal to dipolar arrangement of the electromotive molecules causes that imbalance that manifest itself in a twitch at the make. It is with the return from the dipolar to the natural arrangement, that the organism – to use RITTER'S words – administers itself the Oeffnungsschlag [opening beat].¹⁰²

¹⁰¹ The original German reads: "wie NOBILI die Veränderung durch den absteigenden und aufsteigenden Strom als «Alterazione diretta» und «Alterazione inversa» unterschied, um daran die Auslegung des Gesetzes der Zuckungen zu knüpfen, es klüglich vermeidend, eine Meinung über die Natur jener Veränderung auszusprechen." Du Bois-Reymond. *Untersuchungen über Thierische Elektricität*. Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1849, p. 386.
¹⁰² The original German reads: "Wenn mich nicht alles täuscht, so sind wir jetzt in Stand gesetzt, NOBILI'S Theorie auf eine naturgemäßere Weise zu ergänzen. Meine Meinung, die mir dureh die Thatsachen auferlegt zu sein scheint, ist diese. Wir haben in dem elektrotonischen Zustand jene dauernde Veränderung der Nerven durch den elektrischen Strom wirklich erkannt, deren Dasein zu muthmaßen RITTER, ERMAN und NOBILI allein vergönnt war. Wenn

Du Bois-Reymond's analogy of the action current as an altered state of nerve, which causes induced contractions in the muscle of the frog leg, paralleled the emerging understanding that magnetic force could alter electric force and electric force could drive chemical reactions. Thus, du Bois-Reymond's use of his peripolar molecular theory of electromotive force to account for the phenomena of electrotonus, which he used to describe the state of the nerve action current, follows from the normal science of electrodynamics gaining prominence in the mid-nineteenth century.

Conclusion

German idealists working at Protestant universities endeavored to redefine the Kantian conception of objectivity through their theory of freedom by reframing the subject as a "coming-to-know-itself totality" in which the subject reflects on itself in order to know itself.¹⁰³ The Protestant preoccupation with care of the self helps to explain Romantic ideals of purposefulness and progress, which were reflected in du Bois-Reymond's mid-nineteenth-century experiments as a pursuit for the active mechanism responsible for nerve-muscle interaction. Du Bois-Reymond's attention to neurophysiological change therefore must be considered in light of the Protestant moral imperative.¹⁰⁴

ein Strom auf einen Nerven wirkt, ergeht es letzterem gleich jedem anderen feuchten Leiter. Es wird Elektrolyse eingeleitet, welche mit säulenartiger Polarisation beginnt. Der Uebergang der natürlichen zur dipolaren Anordnung der elektromotorisehen Molekeln bedingt jene Gleichgewichtsstörung, die als Schliefsungszuckung, Schliesungsschmerz sich geltend macht. Die Rückkehr von der dipolaren zur natürlichen Anordnung ist es, wodurch sich der Organismus , um mit RITTER zu reden, den Oeffnungsschlag selber ertheilt. Mit einem Worte, das GALVANI'sche Phaenomen erscheint uns als ein besonderer Fall des von NICHOLSON und CARLISLE entdeckten, durch die Eigenthümlichkeit des thierischen Leiters nur so wunderbar eingekleidet. Galvanische Reizung ist uns nichts mehr als die erste Stufe der Elektrolyse eines Nerven." Du Bois-Reymond. *Untersuchungen über Thierische Elektricität.* Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1849, p. 387. See also Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond.* London: Churchill, 1852, p. 186.

¹⁰³ Limnatis, Nectarios G. *German Idealism and the Problem of Knowledge: Kant, Fichte, Schelling, and Hegel.* Studies in German Idealism, Vol. 8. Edited by Reinier Munk. Springer: 2008, p. 1.

¹⁰⁴ See e.g., Foucault, Michel. *The History of Sexuality, Vol. 3: The Care of the Self.* Translated by R. Hurley. New York: Random House, 1986.

The rise of an idealist philosophy signaled an epistemological shift in thinking about the process of understanding as one which necessitates comparison with the past in order to know the present and achieve the possibilities of the future. In contrast to the Newtonian view of passive mechanism driving the world, idealists embraced an active mechanism. The conception of life forms responding with agency aligned with du Bois-Reymond's articulation of an active material mechanics driving physiological processes, and set up the acceptance of purposefulness at the cellular and molecular level.

An epistemological shift toward making comparisons of activity transpiring between objects, replacing the examination of forms existing in independent slices of time, had to occur in order to make possible a functional study of the nervous system. Du Bois-Reymond's studies of the action current took place during this shift. His use of emerging concepts from galvanism and electrodynamics helped him establish a functional study of the electromotive force in the nerve-muscle preparation of the frog. The science of electrodynamics, including the work of Øersted and Faraday, also must be understood within a *Naturphilosophie* quest to understand nature through the activity of polar forces, guided by a unity of opposites.

According to Kant, we form our experiences by placing things in dynamic relation to each other; understanding dynamic relationships is how we get our way to sure knowledge. We need to see cause and effect, he said, to begin to construct objective knowledge. Kant viewed the Newtonian concepts of attraction and repulsion as the fundamental forces underlying causation. Post-Kantian idealist philosophers conceived of the dynamic activity of attraction and repulsion as nature continuously striving toward its absolute freedom. Through a steady progress toward freedom over time, we would approach the divine within, they said.

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For the idealists, a moral imperative to strive for unconditional freedom drives us to understand the dynamic activity in the universe.¹⁰⁵ Schelling and Hegel's thought represented a move toward reconnecting philosophy with spirituality, linking together again knowledge of the self with transformation of the self for understanding the relationship between the subject and truth. The pursuit of knowledge alone became paramount during what Michel Foucault called the "Cartesian moment," when access to the truth no longer required the moral necessity for inner change.¹⁰⁶ The German Romantic idealist tradition helped resuscitate the interaction between knowledge and inner transformation.

Ritter's electrophysiological experiments on nerve and muscle led to his conception of the nerve's altered state. Ritter incorporated Schelling's philosophy into his experiments, and the emerging idea that there exists different states at different times in nerves parallels the *Naturphilosophie* conception of organic change over time. Du Bois-Reymond, who cited Ritter in his work, participated in the shared puzzle-solving endeavors as many of the physicists and physiologists of the mid-nineteenth century.

Du Bois-Reymond's theory of peripolar molecular rearrangement to account for the phenomena of electrotonus and the negative variation he observed during the action current represents an intersection of electrodynamics with physiology. The conclusions he drew implied that we must know something about the previous state of the nerve to inform its current state; to understand activity, we need a sense of change over time. In short, du Bois-Reymond's experiments opened a space for thinking about the nervous system's adaptability which

¹⁰⁵ Richards, Robert J. "Schelling: The Poetry of Nature." In *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*, 114-192. Chicago: The University of Chicago Press, 2002; Morgan, S. R. "Schelling and the Origins of his *Naturphilosophie.*" In *Romanticism and the Sciences*. Edited by Andrew Cunningham and Nicholas Jardine, 25-37. Cambridge: Cambridge University Press, 1990.

¹⁰⁶ Foucault, Michel. *The Hermeneutics of the Subject: Lectures at the Collège de France 1981–1982*. Edited by F. Gros, translated by G. Burchell. New York: Palgrave Macmillan, 2007.

incorporates history. His work made possible a functional electrophysiological study of the brain and represents a pivotal moment in the pre-history of twentieth-century neuroscience studies of learning and memory.

By the mid-nineteenth century, many Western intellectuals across disciplines understood human history as progressive. We could learn something about ourselves, they said, by learning about past societies. We humans, however, are evolving into better individuals and societies than those of the past. Ideas of social progress paralleled ideas of progression in nature. Revelations from astronomy revealed a changing cosmos. The fossil record tipped people off that the earth had its own history. Learning that geological time was immensely long, as was the history of the universe, culminated in Darwin's theory of biological evolution. The study of neurophysiology, encompassed in the broader field of physiology during the era in which du Bois-Reymond lived, also developed a sense of history, a past, which matters to the current state.

Du Bois-Reymond's studies of animal electricity and discovery of the action current represented an emerging attention to the factor of time as indispensable to understanding the nervous system. His work reveals a turning point at which experimenters of the brain necessarily attended to meaningful physiological change over time. Meanwhile, du Bois-Reymond's friend, Hermann von Helmholtz, having also vowed to disprove vitalism with materialism, engaged with the new epistemology by incorporating thermodynamic principles into his investigations of physiological processes.

Chapter 2

Helmholtz on energy and the biological natural order

In the 1840s, the German physiologist Hermann von Helmholtz (1821-1894), with his friend and colleague du Bois-Reymond, resolved to disprove vitalism—and its metaphysical implications—by adopting a thoroughly materialistic and empirical scientific method in his experimental research. He declared that interpretations of nature should come from experimentation and mathematical reasoning and used his expertise in physics and mathematics to argue that *Lebenskraft*, the vital force, is in fact a set of physicochemical processes subject to the law of energy conservation. The principle of the conservation of energy lent credence to the idea that only causal processes with a physical basis could exist in nature and that no mental acts from the outside could add to the energy of nature.

Du Bois-Reymond brought out the epistemology that emerged out of physics in the world while Helmholtz entered the debate about time and epistemology in physics which transformed discussions of organic nature. By engaging with the laws of thermodynamics to support his argument against vitalism, Helmholtz laid the groundwork for the physiological investigation of organic processes as subject to thermodynamic principles. His experiments studying the capacity for muscular work and the speed of nervous conduction set a precedent for interrogating the sources of energy in living beings as ways for understanding organic functional processing. Together with the British mathematical physicist and engineer William Thomson (1824-1907), Helmholtz's thermodynamic contributions to the investigation of the long history of the earth and the foundations of geology transformed notions of evolutionary time and biology's inherent relationship to earthly measurements.

Vital forces reframed in physical terms

In 1847, Helmholtz presented a soon-to-be famous lecture to the Berlin Physical Society, which he co-founded two years earlier with du Bois-Reymond and several other young German scientists. The lecture argued for an understanding of the basic laws of nature through scientific study of the interactions between matter and the forces which cause matter to be set in motion. Four years later, while working in the Berlin laboratory of experimental physicist Heinrich Gustav Magnus (1802-1870), the Irish-born experimental physicist John Tyndall (1820-1893) bumped into his friend du Bois-Reymond.¹⁰⁷ Du Bois-Reymond gave Tyndall, who in 1853 would become Professor of Natural Philosophy for the Royal Institution of Great Britain, a printed copy of Helmholtz's lecture, insisting "it ought to be translated into English."¹⁰⁸ Tyndall obliged, and in 1853 published it for English readers under the title, "On the Conservation of Force; A Physical Memoir."¹⁰⁹ Helmholtz became a significant link between German and British science in the 1850s and 1860s, cementing the concept of the conservation of energy as a guiding principle for scientific investigation and interpretation across borders and disciplines.¹¹⁰

¹⁰⁷ In his recent biography of Helmholtz, David Cahan said Magnus "stood at the center of Berlin science at midcentury." Through his acquaintance with Magnus, Helmholtz met several scientists, including du Bois-Reymond, who, with Helmholtz, formed the Berlin Physical Society in January 1845. Cahan, David. *Helmholtz: A Life in Science*. Chicago: The University of Chicago Press, 2018, p. 61.

¹⁰⁸ Tyndall, John. "Introduction." In *Popular Lectures on Scientific Subjects*. By H. Helmholtz, translated by E. Atkinson, xv-xvi. New York: D. Appleton and Company, 1885, p. xvi.

¹⁰⁹ The translation was printed on pp. 114-162 in *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals*. Edited by John Tyndall and William Francis. London: Taylor and Francis, 1853.

¹¹⁰ Cahan, David. "Helmholtz and the British Scientific Elite: From Force Conservation to Energy Conservation." *The Notes and Records of the Royal Society*, 66(2012):55-68.

In the lecture-turned-essay, Helmholtz declared, "Force, which originates motion, can only be conceived of as referring to the relation of at least two material bodies towards each other; it is therefore to be defined as the endeavor of two masses to alter their relative positions."¹¹¹ He stressed attendance to the interrelationship between material bodies and their mutual ability to alter one another's motion through space and time as critical to moving past the limitations of a purely mechanical physics which resorted to explanations of "unchangeable attractive and repulsive forces, whose intensity depends solely upon distance."¹¹² According to Helmholtz, a more comprehensive understanding of the laws of nature would include descriptions of the interconvertibility of forces, like how heat develops from the mechanical actions of electricity, for example, as ways to describe motion and the dynamic relationship between objects. With empirical and mathematical evidence that total force must be conserved (i.e., no new force could be created or destroyed), a concept which by the mid-1840s had several supporters, Helmholtz went on to frame the conservation of force in terms of "work" donewhatever amount of work exerted to bring a system from its original state to a subsequent state (like an object gaining heat or increasing in velocity) would equal the amount of work lost should that system be brought back to its original state. At the end of the essay, Helmholtz acknowledged the paucity of knowledge and means for probing forces that are lost and gained in organic processes, and would tackle the issue through physiological experimentation soon after.113

¹¹¹ Helmholtz, Hermann von. "On the Conservation of Force; A Physical Memoir." Translated by John Tyndall. In *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals.* Edited by John Tyndall and William Francis, 114-162. London: Taylor and Francis, 1853, p. 117.

¹¹² Helmholtz, Hermann von. "On the Conservation of Force; A Physical Memoir." Translated by John Tyndall. In *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals.* Edited by John Tyndall and William Francis, 114-162. London: Taylor and Francis, 1853, p. 118.

¹¹³ Helmholtz, Hermann von. "On the Conservation of Force; A Physical Memoir." Translated by John Tyndall. In *Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals.* Edited by John Tyndall and William Francis, 114-162. London: Taylor and Francis, 1853.

As a young scholar, Helmholtz studied Kant and Fichte, and thought he might follow from his father and become a philosopher in his own right. But by 1847, when he delivered his conservation of force lecture, he had embraced the experimental method and physicochemical concepts as the keys to understanding the world. Consequently, Helmholtz did not mention Kant in his essay, and in the opening sentence declared it "independent of metaphysical considerations." Kant's transcendental philosophy no doubt shaped Helmholtz profoundly as he formulated the epistemic concepts outlined in his essay, however, especially in his observance of the laws of causality as guiding principles for understanding interrelated natural phenomena. Although Helmholtz's essay was integral to his materialist project to abolish vitalism, complementing du Bois-Reymond's oeuvre discussed in the previous chapter, it engaged heavily with a German philosophical tradition of searching for a unity of forces in the natural world which emanated from Kant, Leibniz, and the Romantic *Naturphilosophen*.¹¹⁴

The historian of science Norton M. Wise detailed Helmholtz's reframing of Kantian concepts in his conservation of force essay. Helmholtz talked about energy in terms of quantity, not solely intensity, drawing attention to the duality and changeable relations of the concept, as Kant had done for the concept of matter. By thinking mathematically about the range of distances over which two material objects might exert forceful influence over one another's motion, for example, Helmholtz framed material energy as having a quantifiable total potential, even if that energy had not (yet) been spent by producing motion. The *vis viva*, or the energy that

¹¹⁴ Helmholtz, Hermann von. "On the Conservation of Force; A Physical Memoir." Translated by John Tyndall. In Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals. Edited by John Tyndall and William Francis, 114-162. London: Taylor and Francis, 1853; Cahan, David. Helmholtz: A Life in Science. Chicago: The University of Chicago Press, 2018, pp. 66-70; Wise, M. Norton. Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society. Chicago: The University of Chicago Press, 2018, pp. 260-289. For Helmholtz's 1862 views on the relationship between the sciences, philosophy, history, artistic intuition and other ways of accumulating knowledge, see Helmholtz, Hermann von. "On the Relation of Natural Science and General Science." In Popular Lectures on Scientific Subjects. By H. Helmholtz, translated by E. Atkinson, 1-32. New York: D. Appleton and Company, 1885.

an object possesses through its motion (known also as kinetic energy), represented the realized energy working through a system, while the *Spannkraft* represented the total energy capacity, or potential, of that system, whether or not it had been realized (known also as potential energy). Importantly, energy might be expressed mechanically, calorifically, chemically, electrically, magnetically, or electromagnetically, and was convertible through a range of processes.¹¹⁵ Physiological interrogation of the conservation of energy

In 1848, having already completed physiological experiments to measure heat and chemical changes during tetanus (i.e., continuous contraction) of frog muscles, which were attempts to observe conservation of force in the physiological processes of biological tissue, Helmholtz, with enduring help from his wife Olga, began experiments to measure the amount of mechanical work a muscle could produce as a result of brief electrical stimulation to the nerve connected to the muscle. Building upon the work of physiological experimenters who had attempted to measure the force of muscular exertion before him, Helmholtz reasoned that in order to calculate mechanical work, he would measure the distance a muscle could lift a given mass over a given period of time.¹¹⁶ His conservation of force essay showed the relation between the concepts of work and energy, thus his experiments on the measurement of muscular work represented a continuation of the pursuit to examine the conservation of force in physiological processes.

An 1846 article on elastic muscular movement and the thermodynamic interconversions of chemicals to mechanical energy and heat by the German physicist Eduard Weber (1804-

¹¹⁵ Wise, M. Norton. *Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society.* Chicago: The University of Chicago Press, 2018, pp. 278-289.

¹¹⁶ Wise, M. Norton. *Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society.* Chicago: The University of Chicago Press, 2018, pp. 306-319; Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience.* Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, pp. 91-93; See also, Cahan, David. *Helmholtz: A Life in Science.* Chicago: The University of Chicago Press, 2018, pp. 90-92.

1891), who with fellow German physicist and mathematician Carl Friedrich Gauss (1777-1855) invented the first electromagnetic telegraph, demonstrated to Helmholtz the temporal nature of muscular excitation by nerve. Eliciting continuous contraction in muscle, as he had done previously, therefore, was not appropriate, because he had to parametrize time in order to calculate work. Helmholtz, therefore, built a physical apparatus to help him draw a curve of the time course of the rise and fall of muscular effort following instantaneous stimulation of the nerve. Upon contraction, the muscle, which was attached via a rod to a weight of known mass, prompted a stylus (which was also attached to the rod) to simultaneously draw the curve on a sheet of mica, visually revealing a temporality to muscular excitation.¹¹⁷

In late 1849, Helmholtz moved from Berlin to Königsberg and continued his studies on the conservation of force in the nerve-muscle preparation. His experiments on the time course of muscular excitation exposed a time interval, a delay, between electrical nervous stimulation and the initiation of muscular contraction in the frog. Together with Olga, Helmholtz constructed a new apparatus in order to finely measure the minute temporal gap, or the "lost time," observed between stimulus and contraction.¹¹⁸

Through their experiments on muscular work in Berlin, therefore, the Helmholtzes generated a new puzzle to solve upon their arrival in Königsberg—calculating the speed of

 ¹¹⁷ Wise, M. Norton. Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society. Chicago: The University of Chicago Press, 2018, pp. 306-319; Meulders, Michel. Helmholtz: From Enlightenment to Neuroscience. Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, pp. 91-93; See also, Cahan, David. Helmholtz: A Life in Science. Chicago: The University of Chicago Press, 2018, pp. 90-92;
 ¹¹⁸ For more on Helmholtz's development and use of the myograph in the context of the speed of nervous propagation experiments, see Schmidgen, Henning. "Leviathan and the Myograph: Hermann Helmholtz's 'Second Note' on the Propagation Speed of Nervous Stimulations." Science in Context, 28;3(2015):357-396. Wise, M.
 Norton. Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society. Chicago: The University of Chicago Press, 2018, pp. 319-337; Meulders, Michel. Helmholtz: From Enlightenment to Neuroscience. Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, pp. 93-97; See also, Cahan, David. "Scientific Networking." In Helmholtz: A Life in Science, 85-116. Chicago: The University of Chicago Press, 2018, pp. 93-99; Schmidgen, Henning. The Helmholtz Curves: Tracing Lost Time. Translated by Nils F. Schott. New York: Fordham University Press, 2014.

nervous conduction. Helmholtz refined the French physicist Claude S. M. Pouillet's (1790-1868) method of obtaining precise temporal measurements with an electromagnetic galvanometer to the speed of conduction studies. In the 1840s, Pouillet applied a galvanometer in endeavors to synchronize clocks through telegraph lines as well as in pursuits to determine the speed of ballistics. Whereas du Bois-Reymond looked to see whether or not the galvanometer's needle deflected in his studies of the action current, Pouillet's work showed that the magnitude of deflection was proportional to how long an electric current flowed through the physical device.¹¹⁹

Helmholtz delivered electric current to the stimulating nerve and the galvanometer simultaneously, and used a telescope to observe the deflection of the galvanometer needle resulting from muscular contraction, which was proportional in size to the duration of the nervous current. By conducting this experiment repeatedly at various locations along the nerve fiber (with respect to distance from the muscle) and applying statistical calculations to the deflection measurements, Helmholtz computed the speed of nervous conduction to be between 25 to 43 meters per second, far slower than the speed of light, which refuted speculation by his teacher Müller.¹²⁰

¹²⁰ Helmholtz developed a graphical method to depict these results following a poor reception by his peers. The use of statistics made it especially difficult for others to understand, so he created graphs and used a new device, the myograph, to make the results easier to "see." Schmidgen, Henning. "Leviathan and the Myograph: Hermann Helmholtz's 'Second Note' on the Propagation Speed of Nervous Stimulations." *Science in Context*, 28;3(2015):357-396; Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience*. Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, pp. 93-97.

¹¹⁹ Wise, M. Norton. *Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society.* Chicago: The University of Chicago Press, 2018, pp. 319-337; Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience.* Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, pp. 93-97; See also, Cahan, David. "Scientific Networking." In *Helmholtz: A Life in Science,* 85-116. Chicago: The University of Chicago Press, 2018, pp. 93-99; Schmidgen, Henning. *The Helmholtz Curves: Tracing Lost Time.* Translated by Nils F. Schott. New York: Fordham University Press, 2014.

Helmholtz's project to explain everything in terms of physicochemical properties,

including life processes, relied on attention to the temporal relations between cause and effect. His experiments revealed that some unknown process occurs in nerve conduction which slows down its expected velocity and that nerve conduction operates by an additional mechanism or mechanisms which as-yet-known principles of electrical conductance could not explain. His studies brought more attention to the notion of temporality in biology, as William Thomson had done for the notion of directionality.

Thermodynamics and progressive decay

Thomson, who in 1892 became Lord Kelvin, read Helmholtz's conservation of force essay in 1852, after Helmholtz completed his physiological time experiments in frog nerve and muscle, and before publication of Tyndall's English version of the essay. Helmholtz's treatise complemented Thomson's dynamical theory of heat and the new science of energy he helped launch in Britain. The two scientists formulated their ideas during the era of industrialization, and were profoundly shaped by the scientific knowledge accumulated from studying the mechanical work produced by machines. Thus, their concepts of energy also must be understood as intimately connected to cultural ideals of maximizing industrial and economic progress.¹²¹

By the mid-nineteenth century, Thomson was completely devoted to a progressionist view of cosmology and geology, and used the laws of thermodynamics he helped develop to support his views. In 1851, he articulated the second law of thermodynamics, based on the engineering fact that mechanical work led to heat loss. The law of the dissipation of energy,

¹²¹ For a detailed discussion of the ties between scientific knowledge production, culture and industry in Victorian Britain, see Smith, Crosbie. *The Science of Energy: A Cultural History of Energy Physics in Victorian Britain*. Chicago: The University of Chicago Press, 1998. For more on the relationship between the work of Helmholtz and Thomson, see pp. 126-140. See also, Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge University Press, 1989; Wise, M. Norton. *Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society*. Chicago: The University of Chicago Press, 2018.

therefore, is the reason for the impossibility of complete energy efficiency, or of a perpetual motion machine. Thomson reasoned that energy loss by machines demonstrated a universal tendency toward energy loss and a corresponding principle of the irreversibility of the cosmos.¹²² Helmholtz did not possess the same cosmological and theological vision as Thomson, but set out to refute the possibility for vital forces to allow for perpetual motion in his conservation of force essay.¹²³

Helmholtz adapted his concept of force to that of energy thanks in large part to his British associations.¹²⁴ His biographer, neuroscientist Michel Meulders, explained that the concept of energy suited Helmholtz better than the concept of force. Although force causes motion, energy encapsulates the total capacity of a system and its potential to produce work through interconvertible forces. Energy, for Helmholtz, was the sum of kinetic energy, the vital force, and potential energy, the force of tension.¹²⁵ This distinction between kinetic and potential energy came from his physiological studies measuring muscular tension.¹²⁶ In the opening sentences of a lecture titled "On the Application of the Law of the Conservation of Force to Organic Nature," presented to the Royal Institution in the Spring of 1861, Helmholtz himself expressed his preference for the term conservation of energy over conservation of force because energy does not refer to the intensity of force, which does not remain constant, but instead energy "relates more to the whole amount of power which can be gained by any natural process,

¹²² Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge University Press, 1989, pp. 497-502.

¹²³ Wise, M. Norton. "The Mechanism of Matter: Hermann Helmholtz's *Erhaltung der Kraft.*" In *Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society*, 244-298. Chicago: The University of Chicago Press, 2018.

¹²⁴ Cahan, David. "Helmholtz and the British Scientific Elite: From Force Conservation to Energy Conservation." *The Notes and Records of the Royal Society*, 66(2012):55-68.

¹²⁵ Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience*. Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, p. 79.

¹²⁶ Wise, M. Norton. *Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society.* Chicago: The University of Chicago Press, 2018, pp. 278-279.

and by which a certain amount of work can be done."¹²⁷ Energy thus had a temporality to it—a future possibility of more work done—that was not contained in the concept of force and aligned with the concept of progression over time inherent in the second law of thermodynamics, Thomson's principle of energy dissipation.

The sun, according to Thomson, was a perfect example of the cosmical law of dissipation of energy. He channeled the ideas outlined in Helmholtz's 1854 essay "On the interaction of natural forces" when describing the sun as the principal source of heat and therefore of all processes on earth. Unlike Helmholtz, however, Thomson claimed that God placed the initial energy store into the universe. According to Thomson, energy transfer from the sun's store of potential energy, which made possible all the motions of living and nonliving things on earth, could ultimately be attributed to a divine grace creating the initial conditions of a physical universe governed by a principle of decay. He also said that humans possess the special power to direct much of that energy, but can never restore the supply back to its original state.

Consequently, consistent with a general atmosphere of progressivism among intellectuals, which included a break from the 1830s Laplacian notion of a universe in balanced stability, beginning in the 1850s, Thomson expressed his economy of nature as one with directionality—that of progressive decay. Thomson's idea of progress, therefore, hinged on the notion of irreversible decay.¹²⁸ By applying thermodynamic principles to calculate the amount of

¹²⁷ Helmholtz, Hermann von. "On the Application of the Law of the Conservation of Force to Organic Nature." In *Notices of the Proceedings at the Meetings of the Members of the Royal Institution of Great Britain with Abstracts of the Discourses Delivered at the Evening Meetings, Vol. III. 1858-1862, 347-357.* London: William Clowes and Sons, 1862, p. 347. Helmholtz returned to Britain in 1864 (not for the last time) to deliver a series of lectures at the Royal Institution as well as the Croonian Lecture at the Royal Society on the topic of the conservation of energy. He stayed with Thomson, spoke with Faraday and Maxwell, and became widely read by many British intellectuals, including Spencer and Darwin. His writings also shaped the works of Nietzsche and Freud. See, Cahan, David. *Helmholtz: A Life in Science.* Chicago: The University of Chicago Press, 2018, pp. 291-310.

¹²⁸ Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge: Cambridge University Press, 1989, pp. 497-523.

time the sun could feasibly act as a source of heat and light, Thomson estimated the age of the sun to be between 100 and 500 million years.¹²⁹

Following from his project of calculating the age of the sun, which drew from Helmholtz's discussion of the laws of energy conservation and dissipation as guiding principles for understanding the natural order, Thomson argued that the differences in temperature between the earth's hot core and cool crust served as evidence for the earth's continuous loss of heat. To both Helmholtz and Thomson this meant that geological activity diminished over time, and advocated for the theory of catastrophism as an accurate description of the history of geological activity over the uniformitarian theory of Scottish geologist Charles Lyell (1797-1876). Thomson estimated the age of the earth as no more than 100 million years old and his calculations soon became orthodoxy, presenting a problem for uniformitarian geologists studying the fossil record who adopted the position that the history of the earth was near boundless, and correspondingly, that geological processes occur gradually. Thomson's relatively short age estimates were also obstacles to Charles Darwin's biological theory of evolution through natural selection, which rested on the uniformitarian principle of continuity and longer geological timescales to allow for gradual changes as species evolved, little by little.¹³⁰

Geological change and Darwinian biological change

Most eighteenth-century scholars accepted the doctrine of the Great Chain of Being, a pre-established hierarchy of matter and living beings which relied on a belief in fixed and unchanging species. The Great Chain of Being characterized species higher up the chain as

¹²⁹ Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge: Cambridge University Press, 1989, p. 596.

¹³⁰ Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge: Cambridge University Press, 1989, p. 552-611.

closer to Godly perfection, and assumed a precise, unvarying ordering of species.¹³¹ In nineteenth-century natural science, however, the concepts of "emergence" and "process" pervaded, and included heightened attention to directionality and temporality as crucial components to understanding of the biological natural order.¹³² The historian Owsei Temkin argued that the rise of the field of embryology in early nineteenth-century Germany can be linked directly to physiologists incorporating philosophy of history into "a concept of life in which each stage has its definite place."¹³³ At the time, the historical point of view in German embryology assumed a continuity of bodily organization between animal species, with organisms alive at a particular moment in history representing a particular stage of development of the species, which progresses and adapts over time.¹³⁴ As Janina Wellmann shows, the study of embryology helped bring the study of rhythms into biological inquiry. Rhythm became a means of organizing time.¹³⁵ The development of embryology was therefore linked to the idea species transformation. Darwin's specific theory of species transformation was linked to studies of geological history.

Darwin's 1859 publication of *The Origin of Species*, itself a product of the intellectual climate of progressivism, demanded much longer geological time scales to allow for evolution through the slow process of natural selection than Thomson's thermodynamic calculations

¹³¹ Schaffer, Simon. "The Phoenix of Nature: Fire and Evolutionary Cosmology in Wright and Kant." *Journal for the History of Astronomy*, x(1978): 180-200; Toulmin, Stephen, and June Goodfield. "Time's Creative Hand." In *The Discovery of Time*. New York: Harper & Row, 1965, pp. 125-140.

¹³² See, e.g., Richards, Robert J. *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*. Chicago: The University of Chicago Press, 2002.

¹³³ Temkin, Owsei. "German Concepts of Ontogeny and History around 1800." In *The Double Face of Janus and Other Essays in the History of Medicine*, 373-389. Baltimore: The Johns Hopkins University Press, 1977, p. 374. ¹³⁴ Note the parallels to Darwin's evolutionary theory. This line of thinking preceded Darwin. Temkin, Owsei.

[&]quot;German Concepts of Ontogeny and History around 1800." In *The Double Face of Janus and Other Essays in the History of Medicine*, 373-389. Baltimore: The Johns Hopkins University Press, 1977.

¹³⁵ Wellmann, Janina. *The Form of Becoming: Embryology and the Epistemology of Rhythm*, 1760-1830. Cambridge, MA: The MIT Press, 2017.

permitted. Thomson, a physicist, help set the limits for geological time through his advocacy of the dissipation of energy principle, opposing steady-state uniformitarian geologists like Lyell. He also argued against Darwin's theory of natural selection by chance because it conflicted with his idea of intelligent design in the sense that God directed the origin of life by allowing progression through decay.¹³⁶ As the historian Peter Bowler shows, however, Thomson eventually lost the debate about evolution through natural selection, due in part to the discovery of radioactivity which massively elongated projected timescales of energy decay. Darwin's theory, which incorporated the Lyellian, uniformitarian notion of gradual change, but did not include its assertion of a steady-state earth (which had been discredited by proponents of directionalism), soon became orthodoxy.¹³⁷ Thus, the progressive nature of Thomson's cosmological vision together with Darwin's biological order, which depends on earth's long history, remain and continue to influence socioscientific investigation today.

Conclusion

Helmholtz's measurements of muscular work capacity and nerve fiber conduction speed fit in with his project to prove a conservation of energy in organic life processes. His experiments highlighted the notion of work for the measurement of energy and the corresponding need for a sense of time to understand work done. Helmholtz contributed to the debate about time and epistemology which subsequently transformed discussions about organic nature via the investigation of the history of the earth and the foundations of geology.

¹³⁶ Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge: Cambridge University Press, 1989, p. 552-611.

¹³⁷ Bowler, Peter J. *Evolution: The History of an Idea.* Third Edition. Berkeley: University of California Press, 2003, pp. 7-13, 96-223. See also, Archibald, J. David. "Marking Time." In *Origins of Darwin's Evolution: Solving the Species Puzzle Through Time and Place*, 44-58. New York: Columbia University Press, 2017; Allen, Garland. "The History of Evolutionary Thought." In *The Princeton Guide to Evolution.* Edited by Jonathan B. Losos, et al., 10-27. Princeton: Princeton University Press, 2013; Rudwick, Martin J. S. *Earth's Deep History: How it Was Discovered and Why it Matters.* Chicago: The University of Chicago Press, 2014.

Studies using thermodynamic principles to explain the biological natural order and geological natural order interacted to produce a theory of the evolution of species on the basis of natural selection. The concepts of historical progression, change over time, and the progression and change of species were not new to Darwin, as evidenced by the progressive cosmological vision of Thomson. Indeed, Hegel, Schelling, and Goethe were friendly to these evolutionary ideas at end of the eighteenth century.¹³⁸

Darwinian evolution allowed for an acceptable version of organic teleological progress and the notion of evolutionary time prefigured biology and provided an explanatory mechanism for adaptive nature. Beginning in the twentieth century, following from Helmholtz's investigations of the principle of energy conservation in biological phenomena and shaped also by the Darwinian notion of evolution, Charles Sherrington and his colleagues discussed and investigated the energy sources of nervous conduction and transmission in adaptive evolutionary terms through their reductionist neurophysiological project, while assuming the inherent orderliness of nature that Darwin, Herbert Spencer, and John Hughlings Jackson promulgated.

¹³⁸ Richards, Robert J. "Did Goethe and Schelling Endorse Species Evolution?" In *Marking Time: Romanticism and Evolution*. Edited by Joel Faflak, 219-238. Toronto: University of Toronto Press, 2017; Rajan, Tilottama. "The Vitality of Idealism: Life and Evolution in Schelling's and Hegel's Systems." In *Marking Time: Romanticism and Evolution*. Edited by Joel Faflak, 239-269. Toronto: University of Toronto Press, 2017.

Chapter 3

Sherrington and company refine the electroconductive model

Today, neuroscientists take for granted the presence of electrical current and voltage change as synonymous with the action potential, the nervous impulse. But in the early part of the twentieth century this was not a given and was at times contested. Emil du Bois-Reymond described the action current in terms of electromotive force, but the exact nature of the relationship between electromotive force and the action current remained a driving question amongst neurophysiologists through the mid-twentieth century.

The question of the generation of the impulse was really a question about energy. Twentieth-century neurophysiologists asked, following from the conservation of energy discourse initiated by Helmholtz the century prior: Where does the impulse get its energy to propagate? How does it propagate? What *is* the impulse? And how does electrical excitability relate to nervous activity? They knew that electrical conductance accompanied the impulse, but could not (or would not) say if they were one and the same, not until the Hodgkin-Huxley model of electrical conductance across the neuronal membrane settled the issue.

Before twentieth-century neurophysiologists reengaged with these questions using new technology to observe and measure small electrical changes in organic matter, the English neurophysiologist Charles Scott Sherrington (1857-1952), following from nineteenth-century neurological discourse shaped by evolutionary ideas, asked broader questions about how the nervous system functions as a whole from an assemblage of interconnected and intricately

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controlled parts. His concepts help set the groundwork for investigations into the biophysical properties of neurons—at that time understood as the fundamental units of nervous activity which underpinned the regulation of animal behavior—and their temporal and conductive relations. Sherrington's method of physiologically studying the nervous system depended on his notion of integrative action. He sought to understand how through their electrical conductivity nerve cells, or neurons, combine activity to form a unified, whole-behaving animal. Together with his twentieth-century colleagues Sherrington helped eliminate Cartesian language referencing "vital spirits" from the study of neurophysiology, replacing it with language of activity, adaptation, regulation, control, coordination, and organization which was grounded in a reductive materialist model of the nervous system and predicated on the assumption that "the universal goal of animal behavior" is "to dominate more completely the environment."¹³⁹

Through their research and interpretation of reflex arcs and synapses, the temporal relations and biophysical properties of neurons as well as neuronal membrane permeability and the generation and propagation of the action potential (formerly the action current, but also known as the nervous impulse or discharge), the neurophysiologists discussed in this chapter finally disposed of the concept of an "informing spirit" inhabiting an organism, a project which had been started by du Bois-Reymond, Helmholtz and their colleagues the century prior. The collective work of these twentieth-century neurophysiologists, extending from the investigations of du Bois-Reymond and Helmholtz, represents more than a paradigm shift in neurophysiological research; it amounts to a philosophical shift, a metaphysical stance insisting on the material nature of both the body and the mind which was reached incrementally as a consequence of their scientific studies.

¹³⁹ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, p. 353.

The reflex and the synapse

Charles Scott Sherrington was born in 1857 in the Greater London district of Islington and spent most of his childhood years in Ipswich, a town to the northeast of London in the county of Suffolk. He undertook medical studies in London, trained for a brief period in Edinburgh, and completed his undergraduate education in physiology at Cambridge in 1885. Writing upon Sherrington's death in 1952, his student, the English neurophysiologist Edward G. T. Liddell (1895-1981) said that Sherrington arrived at Cambridge "when much was afoot in England in the field of physiology and experimental medicine. The German universities were spreading their knowledge abroad."¹⁴⁰

Sherrington spent some time in Germany, working briefly under the German pathologist Rudolf Virchow (1821-1902) and staying about a year with the German bacteriologist Robert Koch (1843-1910). Following that, Sherrington periodically returned to Strasbourg, France, enjoying the guidance of the German physiologist Friedrich Goltz (1834-1902). Sherrington went on to a long and prolific career in neurophysiology, serving as Chair of Physiology at Liverpool from 1895 until 1913 when he moved to Oxford. He retired in 1936 at the age of 79.¹⁴¹

Sherrington's interest in studies of the nervous system trace back to the 1881 International Medical Congress held in London where he witnessed presentations by Goltz and the British neurologist David Ferrier (1843-1928). Goltz's demonstration of an apparently unaffected dog despite having cortical tissue removed supported his doubt in cortical localization of function. Ferrier, in contrast, argued in favor of it, brandishing two monkeys with surgically-

¹⁴⁰ Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs of Fellows of the Royal Society*, 8;12(1952):241-270, p. 242.

¹⁴¹ Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs of Fellows of the Royal Society*, 8;12(1952):241-270; Fulton, J. F. "Sir Charles Scott Sherrington, O.M. (1857-1952)." *The Journal of Neurophysiology*, 15(1952):167-190; Fulton, J. F. "Sherrington's Impact on Neurophysiology." *British Medical Journal*, (1947):807-810.

induced cerebral lesions—one was made deaf and the other exhibited hemiplegia, paralysis on one side of the body. Following contentious debate, Sherrington and the British physiologist J. N. Langley (1852-1925) took the right hemisphere of Goltz's dog back with them to Cambridge; they published a paper together on it in 1884, Sherrington's first. Liddell noted: "There were at the time many questions, and few answers, but Goltz and Ferrier had shown that experimental method might help to provide answers. Experimental medicine was definitely on the move."¹⁴²

Later in life Sherrington dedicated his time to historical and philosophical scholarship. During World War II he wrote a biography of the sixteenth-century French physician, physiologist and philosopher Jean Fernel (1497-1558), a musing on the German Romantic writer Johann Wolfgang von Goethe's (1749-1832) stance on the relationship between the natural sciences and the natural world, and published his own philosophical reflections titled *Man on his Nature* in which he asserted the difference between Mind and Nature. In that book he also described human nature as in a process of becoming and argued that scientists are in the business of describing *how*, not explaining *why* nor passing judgments on what is good or bad.¹⁴³

Sherrington's studies of reflex physiology informed his influential 1906 monograph *The Integrative Action of the Nervous System* (first delivered at Yale in 1904 as a series of ten Silliman Lectures) which outlined his overarching theory about the nervous system's coordination of simple reflexes to create complex behaviors and their psychical adjuncts. The British neurologist Francis M. R. Walshe (1885-1973) compared *Integrative Action* with Isaac Newton's (1642-1727) *Principia*, the three-volume treatise on the universal laws of gravity and

¹⁴² Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs of Fellows of the Royal Society*, 8;12(1952):241-270, p. 242. See also, Fulton, J. F. "Sir Charles Scott Sherrington, O.M. (1857-1952)." *The Journal of Neurophysiology*, 15(1952):167-190.

¹⁴³ Sherrington, Charles S. *The Endeavour of Jean Fernel*. Cambridge: Cambridge University Press, 1946; Sherrington, Charles S. *Goethe on Nature and on Science*. Cambridge: Cambridge University Press, 1942; Sherrington, Charles S. *Man on his Nature*. The Gifford Lectures, Edinburgh, 1937-1938. New York: The Macmillan Company, 1941.

motion; the American physiologist John F. Fulton (1899-1960) ranked *Integrative Action* with William Harvey's (1578-1657) *Du Motu Cordis*, the famous work of physiology and anatomy describing the circulation of the blood, claiming *Integrative Action* "marked a turning-point in the history of physiological thought."¹⁴⁴

Helmholtz's speed of nerve conduction discovery and measurements of the time delay between application of an electric shock on a nerve and the contraction of muscle, part of his project to demonstrate the law of the conservation of energy in organic systems, prompted some to speculate on the "lost time" between nerve conduction and reflex time. Sherrington, based on his experimental observations that nerve degeneration was limited, not diffuse, sided with his friend Spanish anatomist Santiago Ramón y Cajal (1852-1934) in his debate with Italian biologist Camillo Golgi (1843-1926; who shared the Nobel Prize with Ramón y Cajal in 1905) about whether the brain consisted of individually-confined cells or a diffuse nerve-net. Convinced by Ramón y Cajal's individual neuron doctrine, Sherrington postulated the existence of a functional junction, or synapsis (later, synapse), between nerve cells which could account for the "lost time" in reflex action.¹⁴⁵ In *Integrative Action* Sherrington presented synapses as active integrators of inhibitory and excitatory information in the nervous system; they mediate *inter*cellular phenomena, linking together the nervous system's individual living units—neurons. Synapses, theorized Sherrington, help to connect and coordinate reflex action, which is the basis for all activity in the brain, including emotions. Sherrington defined a reflex as the reaction of an

¹⁴⁴ Walshe, F. M. R. "Reviews: A Foundation of Neurology." *British Medical Journal*, (1947):823; Fulton, J. F. "Sherrington's Impact on Neurophysiology." *British Medical Journal*, (1947):807-810, p. 807.

¹⁴⁵ Finger, S. "Charles Sherrington: The Integrated Nervous System." In *Minds Behind the Brain: A History of the Pioneers and Their Discoveries*, 217-237. Oxford: Oxford University Press, 2004; Swazey, Judith P. "Sherrington's Concept of Integrative Action." *Journal of the History of Biology*, 1;1(1968):57-89; See also, Eccles, J. C., and W. C. Gibson. *Sherrington: His Life and Thought*. New York: Springer International, 1979; Granit, R. *Charles Scott Sherrington: An Appraisal*. Garden City, NY: Doubleday, 1967; Denny-Brown, D. "The Sherrington School of Physiology." *Journal of Neurophysiology*, 20(1957):543-548.

organism that occurs when an environmental stimulus initiates activity in a receptor organ and is then mediated through a conductor to create a reaction in an effector organ. This chain of structures—receptor, conductor and effector—comprise a reflex-arc.¹⁴⁶

In the final decade of the nineteenth century, Sherrington engaged in animal experiments testing spinal reflexes. He wanted to address directly the controversy about whether the knee-jerk reflex—which seemed to occur too quickly to be a true reflex—was indeed a true reflex (i.e., whether it was the output of a reflex arc pathway passing through the spinal cord) or whether it was a direct muscular reaction to tonus contraction in the muscle. Sherrington's work, which made use of sectioning (i.e., severing) or stimulating the nerves to the antagonistic muscles of rabbits, cats and monkeys previously thought not concerned in the knee-jerk reflex, pointed to the novel idea that muscles send afferent signals *back* to the spinal cord roots to effect reflex output—an early concept of reflex inhibition.¹⁴⁷

In the years following, Sherrington concerned himself primarily with (1) mapping out the anatomical pathways of nerves to and from the spinal cord, and (2) attempting to understand the functional behavior of reflexes—how muscles acted together via impulses to and from spinal nerves. In the latter capacity Sherrington followed from Scottish anatomist surgeons and brothers Charles Bell (1774-1842) and John Bell (1763-1820), who thought that nerves might be doing something other than stimulating muscles as they observed an extensor muscle relax while its partner flexor muscle contracted. Sherrington used the phrase "reciprocal innervation" to explain

¹⁴⁶ The conductors are the nerves (individually, neurons). Sherrington, Charles S. "Lecture I: Introductory – Coordination of the Simple Reflex." In *The Integrative Action of the Nervous System*, 1-35. New York: Charles Scribner's Sons, 1906.

¹⁴⁷ Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs of Fellows of the Royal Society*, 8;12(1952):241-270; Sherrington, Charles S. "Note Toward the Localisation of the Knee-Jerk." *British Medical Journal*, 1;1628(1892):545.

the action of antagonistic muscles.¹⁴⁸ Although Sherrington's vision for understanding the integration of reflexes as the key to understanding the whole behavior of an organism did not come to fruition, his systematic work on spinal reflex physiology and the concepts that emerged—particularly that of reciprocal innervation—informed his idea of integration at the synapse as a mechanism for coordinating and combining simple reflexes into more complex ones and stimulated subsequent research on the electrophysiology of nervous conduction and transmission.¹⁴⁹

In his 1904 Presidential Address to the Section of Physiology at the annual meeting of the British Association for the Advancement of Science, Sherrington shared the "three main points of view" from which physiology studies the nervous system.¹⁵⁰ The first was from its processes of nutrition—trying to understand how nerve cells, as individual living units, "dispense their own stores of energy."¹⁵¹ The same methods used to study nutrition in other cells, and the body as a whole, could be applied to nerve cells, he said. The second approach to studying the physiology of the nervous system involved examining the specific property which characterizes and distinguishes nerve cells from other cells in the body—its conductivity (i.e., its ability to conduct electric current). According to Sherrington, the "intimate nature" of conductivity is "a problem coextensive with the existence of nerve-cells, and enters as a factor into every question

¹⁵⁰ Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In *Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science*, 728-741. London: John Murray, 1905, p. 728.

¹⁴⁸ Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs of Fellows of the Royal Society*, 8;12(1952):241-270.

¹⁴⁹ Fulton, J. F. "Sherrington's Impact on Neurophysiology." *British Medical Journal*, (1947):807-810, p. 808. Denny-Brown, D. "The Sherrington School of Physiology." *Journal of Neurophysiology*, 20 (1957):543-548.

¹⁵¹ Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In *Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science*, 728-741. London: John Murray, 1905, p. 728.

concerning the specific reactions of the nervous system."¹⁵² Neurophysiology research described below which investigated the temporal relations and biophysical properties of nerves and individual neurons and attempted to relate membrane conductivity with the process of electric excitation represents the combination of these first two points of view defined by Sherrington.

According to Sherrington, the third way of physiologically studying the nervous system was to ask "how by its 'conductivity' the separate units of an animal body are welded into a single whole, and from a mere collection of organs there is constructed an individual animal."¹⁵³ Sherrington called this the *integrative function* of the nervous system, and its unit mechanism was the reflex. Through work with animals—rabbits, dogs, cats, monkeys—and eliciting their reflexes—the knee-jerk reflex, the scratch reflex, hip-extensor reflexes—reflex physiologists like Sherrington studied conduction occurring along a reflex chain: from a receptor organ (an area of skin, for example) through the spinal cord to the final or efferent motor neuron, which elicits movement of muscle.

Sherrington admitted the field of neurophysiology was "much in need of data derived from the two previously mentioned lines of study" (i.e., where the neurons get their energy and how they conduct electricity).¹⁵⁴ But his goal was to demonstrate the nervous system's functional unity, that it was an integrated whole operating through a complex organization of interacting reflex arcs. Neurophysiologists following him, however, admitting the lack of knowledge base and suitable tools needed to achieve a comprehensive understanding of the nervous system's

¹⁵² Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In *Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science*, 728-741. London: John Murray, 1905, p. 728.

¹⁵³ Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In *Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science*, 728-741. London: John Murray, 1905, p. 728.

¹⁵⁴ Sherrington, Charles S. "Lecture I: Introductory – Co-ordination of the Simple Reflex." In *The Integrative Action of the Nervous System*, 1-35. New York: Charles Scribner's Sons, 1906, p. 2.

integrative action, repositioned the field toward tackling those first two lines of inquiry in hopes their reductive approach would help future generations form a more comprehensive theory of nervous system function.

Sherrington's conception of nervous system functionality and control outlined in *Integrative Action* must be understood in light of nineteenth-century research on the reflex, much of which attempted to demonstrate the uniformity of nervous function and which was itself an outgrowth of the *Naturphilosophie* search for a unified life science, embraced most fiercely in German-speaking states but which also had its proponents in Britain and France.¹⁵⁵ Sherrington combined the orderliness from the French philosopher Descartes, British philosopher Herbert Spencer (1820-1903) and the British neurologists John Hughlings Jackson (1835-1911) and David Ferrier—to whom he dedicated *Integrative Action*—into an emerging interest in temporal dynamics owing to the rise of physiologists like du Bois-Reymond and Helmholtz who merged contemporary physics with biological experimentation.

Sherrington expressed the function of the reflex as having teleological purpose in terms of adaptation driven by evolutionary processes. "The effect of any reflex," said Sherrington, "is to enable the organism in some particular respect to better dominate the environment." According to Sherrington, "higher" organisms (like humans) were those whose reflex reactions were the "more numerous and extensive," allowing them to "figure out" the outside world better than "lower" creatures, with their less-developed repertoire of reflex reactions.¹⁵⁶ Sherrington's words mirrored an anthropological and sociological hierarchy of the idea of higher order brain functions controlling primitive ones.

¹⁵⁵ Clarke, Edwin, and L.S. Jacyna. *Nineteenth-Century Origins of Neuroscientific Concepts*. Berkeley: University of California Press, 1987, pp. 1-4, 101-156.

¹⁵⁶ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, pp. 236-237.

Sherrington's neurophysiology was shaped by trends in physics, biochemistry, anatomy and the Darwinian imperative popularized in late nineteenth-century Britain by the philosopher Herbert Spencer, whom he cited in *Integrative Action*. Spencer, shaped by the work of French philosopher Auguste Comte (1798-1857), emphasized the organism-environment relationship as one in which the organism constantly changes and adapts its internal processes through its interaction with and in response to changes in the external world.¹⁵⁷A proponent of free enterprise capitalism and possessing an individualistic ideology, Spencer was sympathetic to the Lamarckian evolutionary notion that active and innovative individual organisms pass along acquired characteristics from one generation to the next. He departed from Darwin's notion of evolution through natural selection driven by chance when espousing a conception of evolution as inevitably and progressively developing toward higher levels of complexity over time. For Spencer, the evolution of the mind and the corresponding transformation from nervous system homogeneity found in "lower" organisms toward the maximum heterogeneity and differentiation of the human nervous system meant humans were capable not only of the most complex movements and reactions, but also explained the complexity of human society. Mental and social evolution, furthermore, would drive each other toward progressively greater levels of development.¹⁵⁸ In *The Principles of Psychology*, Spencer noted that the level of integration and heterogeneity in a nervous system reflects its number and complexity of links and connections.¹⁵⁹

¹⁵⁷ Spencer, Herbert. *The Principles of Psychology*, Vols. I and II. New York: D. Appleton and Company, 1873; Pearce, Trevor. "The Origins and Development of the Idea of Organism-Environment Interaction." In *Entangled Life: History, Philosophy and Theory of the Life Sciences*. Edited by G. Barker et al., 13-32. Dordrecht: Springer Science, 2014.

¹⁵⁸ Bowler, Peter J. "The Eclipse of Darwinism: Scientific Evolutionism, 1875-1925." In *Evolution: The History of an Idea*. Third Edition, 177-223. Berkeley: University of California Press, 2003; Blitz, David. "Herbert Spencer: Philosophy of Evolution." In *Emergent Evolution: Qualitative Novelty and the Levels of Reality*, 24-34. Dordrecht: Springer Science, 1992.

¹⁵⁹ Spencer, Herbert. "The Functions of the Nervous System." In *The Principles of Psychology*, Vol. I, 48-67. New York: D. Appleton and Company, 1873.

When discussing the nervous system's ability to integrate multiple reflexes originating from different segments of the body, Sherrington wrote, "Here it is that we see eminently what Herbert Spencer has insisted on, namely, that integration keeps pace with differentiation."¹⁶⁰

John Hughlings Jackson, concerned with the dynamic processes of central nervous system function and dysfunction when his colleagues were concerned with topographical representation of movement in the cortex, attempted to bridge functional and organic models of disease. Sherrington's concept of integrative action to explain nervous function refreshed Jackson's release of function concept which the latter used to explain clinical cases of hemiplegia (i.e., paralysis on one side of the body).¹⁶¹ In the 1870s Jackson became skeptical that the idea of the reflex arc, which linked sensory and motor function, could be extended to understand "higher order" mental processes and other parts of the brain like the language center the French physician and anatomist Paul Broca (1824-1880) had recently identified. Following from Spencer, Jackson maintained all that could be localized in the cortex are sensations and movements. As a solution, Jackson adapted his philosophy of "parallelism" which maintained that physiological processes occurred at the same time as (in parallel with) mental processes.¹⁶²

¹⁶¹ On p. 303 of *Integrative Action*, Sherrington praised Jackson's "characteristic penetration of thought" when citing Jackson's attribution of hemiplegia to a loss of antagonism to the cerebellum. See also Fulton, J. F. "Sherrington's Impact on Neurophysiology." *British Medical Journal*, (1947):807-810, p. 809.

¹⁶² The experiments of German physiologists Gustav Fritsch and Eduard Hitzig in the 1870s as well as those of the British neurologist David Ferrier demonstrated the topographic arrangement of motor function in the cerebrum and supported the doctrine of cerebral localization of function. The German psychiatrist Carl Wernicke helped explain localization of function in terms of the eighteenth-century psychological laws of association. Jacyna, Stephen L. "Process and Progress: John Hughlings Jackson's Philosophy of Science." *Brain*, 134(2011):3121-3126; Harrington, Anne. "The Brain and the Behavioral Sciences." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences*. Edited by Peter J. Bowler and John V. Pickstone, 504-532. Cambridge: Cambridge University Press, 2009. See also, Young, Robert Maxwell. *Mind, Brain and Adaptation in the Nineteenth Century*. New York: Oxford University Press, 1970; Harrington, Anne. *Medicine, Mind and the Double Brain*. Princeton: Princeton University Press, 1987.

¹⁶⁰ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, p. 344.

In his 1884 Croonian Lectures delivered to the Royal College of Physicians in London, Jackson explicitly applied Spencer's concept of evolution to the nervous system. Based on clinical cases and his studies of epilepsy, Jackson considered disease as reversals of evolution, or dissolution, a word he borrowed from Spencer. Jackson maintained that the evolutionary passage from the simple to more complex, from more automatic to more voluntary behavior can be illuminated by the organization of the nervous system. The highest nervous centers are the "climax of nervous evolution" and are the least organized, but have the most control, he said. The less organized (or, in Spencerian terms, more heterogenous) cortex is actually more evolved, according to Jackson, and allows for learning over the course of an individual's life. Furthermore, he said the hierarchy in the brain parallels hierarchy of the social order:

The doctrine of evolution implies the passage from the most organised to the least organised, or, in other terms, from the most general to the most special. Roughly, we say that there is a gradual "adding on" of the more and more special, a continual adding on of new organisations. But this "adding on" is at the same time a "keeping down." The higher nervous arrangements evolved out of the lower keep down those lower, just as a government evolved out of a nation controls as well as directs that nation. If this be the process of evolution, then the reverse process of dissolution is not only "a taking off" of the higher, but is at the very same time a "letting go" of the lower. If the governing body of this country were destroyed suddenly, we should have two causes for lamentation: 1, The loss of services of eminent men; and 2, the anarchy of the now uncontrolled people. The loss of the governing body answers to the dissolution in our patient (the exhaustion of the two highest layers of his highest centres); the anarchy answers to the no longer controlled activity of the next lower level of evolution (third layer).¹⁶³

¹⁶³ Jackson, John Hughlings. "The Croonian Lectures on Evolution and Dissolution of the Nervous System. Lecture II." *The British Medical Journal*, 1;1214(1884):660-663, p. 662.

Jackson's conception of the brain as hierarchically-structured provided a framework for explaining how it keeps a historical record of its own evolving nature. For Jackson, the brain was not solely a material object but a snapshot of a process evolving in time. The historian Anne Harrington asserted that Jackson's doctrine of evolution, which posited the "higher" centers—those responsible for the human capacities for reasoning and morality—as most recently evolved and less organized also meant that they were the most vulnerable to breaking down. Jackson's fear of dissolution, the state of functionality that would occur when "lower" brain centers took over, must be contextualized within the era of social instability and political turmoil in which Jackson lived.¹⁶⁴

What the cerebrum (i.e., cortex) does differently from the peripheral motor tract, said Jackson, is account for changes in movements, which requires the intricate coordination of movements and impressions in time and space. Instead of localizing the four faculties—will, reason, memory, and emotion—in the cortex, Jackson said that consciousness—a combination of the four artificially distinguished faculties—arises during the coordination of activity in the highest centers of the cerebrum. The least organized centers (i.e., the "highest" centers) are that way to allow for "new acquirements" and account for change over time in the brain. Jackson also believed that humans have more evolving to do, and that we have a moral imperative to evolve. The process of internal evolution, he maintained, would be most active in the "highest" cortical centers.¹⁶⁵

¹⁶⁴ Harrington, Anne. "The Brain and the Behavioral Sciences." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences.* Edited by Peter J. Bowler and John V. Pickstone, 504-532. Cambridge: Cambridge University Press, 2009, p. 517.

¹⁶⁵ Sherrington summarized Jackson's position on the cerebrum's ability to account for changes in movements on p. 303 in *Integrative Action*. Jackson, John Hughlings. "The Croonian Lectures on Evolution and Dissolution of the Nervous System. Lecture III." *The British Medical Journal*, 1;1217(1884):739-744.

Darwin, Spencer, Jackson, Ferrier, Goltz and many others informed Sherrington and his work. He accepted the hierarchy of species and the assumption of hierarchical control in the brain. He believed that our enhanced capacity to quickly and adaptively engage with the environment is what makes us special as humans. Sherrington agreed with his predecessors that the cortex is the most dynamic and necessarily least organized part of the brain; its power lay in its ability to coordinate and control the various types of information coming in from the more rigid, primitive and reflexive parts of the nervous system. Jackson's insistence that the cortex is the least organized yet also most complex part of the brain laid in his belief that that the cortex is necessarily flexible and plastic in its organization so that it can direct the body in performing voluntary behaviors on-the-fly instead of producing a repertoire of rigid, automatic behaviors that could not evolve or improve. Importantly, this cerebral power demanded a sense of timekeeping. In the first Sherrington Memorial Lecture delivered a century after Sherrington's birth, the English neurophysiologist Edgar Douglas Adrian (1889-1977), who would share the Nobel Prize with Sherrington in 1932, summarized the importance of Sherrington's work and thought.¹⁶⁶ Although Sherrington and Adrian did not collaborate experimentally, they headed neurophysiological research at Oxford and Cambridge, respectively, and enjoyed a collegial relationship that lasted nearly half a century.

Temporal relations and biophysical properties

By 1904, when Sherrington delivered his Presidential Address, several workers had already contributed to understanding the conductive patterns, or anatomical paths, which could lead to a variety of reflex responses. They knew, for example, that one receptive point might

¹⁶⁶ Adrian, E. D. "The Analysis of the Nervous System." *Proceedings of the Royal Society of Medicine*, 50(1957):991-998.

connect to multiple muscles or glands via distinct reflex arcs, but that the distinct reflex arcs converge on a single shank which conducts from the periphery to the central nervous system. From there, conduction could occur along a vast network of paths, each with manifold connections—reinforcing the idea of the central nervous system, and specifically the cerebrum, as the seat of control.

Sherrington noted, however, that schemata constructed by previous workers of the anatomical conductive paths and patterns did not account for temporal data. It was crucial, he said, to understand that "the pattern is unstable, the details of connection shift from moment to moment. We might compare the central organ with a telephone exchange, where from moment to moment the connections between starting and end points are changed to suit passing requirements. In order to realise the exchange at work, one has to add to its purely spatial plan the temporal datum that within certain limits the connections of the lines shift to and fro."¹⁶⁷ Sherrington's metaphor of a telephone exchange reflected emerging technology of his era and also reveals his conception of nervous patterns as necessarily transpiring along predefined routes which remained in place indefinitely, as did telegraph cables once physically installed. Yet the metaphor also allowed for the idea that attending to temporal data could reveal that information gleaned about the nervous system at one point in time might not hold at another time, just as relay switches along the telegraph system permitted varied transmissions of information.

Studying the temporal dynamics of nervous conduction, asserted Sherrington, was integral to understanding how change occurs in the nervous system. Distinct reflex arcs which use the same conductive paths might interact by mutually reinforcing each other's action *or* by

¹⁶⁷ Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In *Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science*, 728-741. London: John Murray, 1905, p. 739.

inhibiting one reflex action altogether. "Expressed teleologically," said Sherrington, "the common path, although economically subservient for various purposes, is yet used only for one purpose at a time."¹⁶⁸

Key concepts outlined in Sherrington's early work on reflex physiology, which focused on correlating anatomical with functional relationships, shaped subsequent work on nervous conduction. Sherrington's *Integrative Action* provided a framework for interrogating the mechanistic nature of nervous conduction and transmission and allowed scientists—with the aid of new technology—to formulate new questions and set about tackling them.

A shift from measuring how activity of specific nerve pathways affects the contraction of muscle (i.e., reflex physiology) to measuring the nuances of fibers' electrically conductive properties (i.e., biophysics) opened up a new research paradigm, a different set of research practices aimed at describing the electrical properties of nerve fibers and uncovering the mechanism underlying the generation and propagation of electrical activity in nerves. Neurophysiologists in the first half of the twentieth century produced and legitimized scientific knowledge about the functioning of the nervous system at the cellular level with concepts and tools from physics and chemistry. They engaged in research projects to elucidate the dynamic electrical properties of nerve fibers and their action potentials—e.g., time constants, membrane potentials, conductances, resistances, and frequencies of discharge—under various conditions— e.g., in the presence of poisons and changes in electrical stimulation strengths and frequencies, temperature, and ionic composition of the aqueous bath surrounding the experimental

¹⁶⁸ Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In *Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science*, 728-741. London: John Murray, 1905, p. 739.

preparation.¹⁶⁹ These projects ultimately boiled down to a desire to answer the questions – how do a nerve's electrical properties relate to its function and where do these electrical properties come from in the first place?

Owing to advances in wireless telegraphy from World War I, Adrian used emerging technology to more finely measure and analyze the small electrical signals produced by neurons—technology Sherrington did not yet have for his experiments leading to *Integrative Action*—which gave Adrian his Nobel Prize.¹⁷⁰ In 1904, the English electrical engineer John Ambrose Fleming (1849-1945), working in wireless telegraphy, figured out how to convert weak alternating current (electrons flowing in both directions across a metal wire) to pulsing direct current (electrons which flow in only one direction) using thermionic emission. By applying battery-supplied current, Fleming could control the flow of electrical current "as a valve in a water-pipe acts towards a current of water."¹⁷¹ In 1907 the American inventor Lee de Forest (1873-1961) introduced a method to *amplify* current—a critical addition for future physiologists attempting to detect extremely small currents across individual nerve cells.¹⁷²

In the 1910s, Adrian, in collaboration with the English neurophysiologist Keith Lucas (1879-1916), found that "inadequate" electric currents in nerve and muscle, despite exhibiting a "local excitatory process," did not always result in "propagated disturbances" (i.e., contraction in the muscle or discharge in a nerve).¹⁷³ Adrian and Lucas' result contributed to the "all-or-none"

 ¹⁶⁹ See e.g., Finger, S. "Otto Loewi and Henry Dale: The Discovery of Neurotransmitters." In *Minds Behind the Brain: A History of the Pioneers and Their Discoveries*, 259-279. Oxford: Oxford University Press, 2004.
 ¹⁷⁰ Bradley, J. K., and E. M. Tansey. "The Coming of the Electronic Age to the Cambridge Physiology Laboratory:

E. D. Adrian's Valve Amplifier in 1921." *Notes and Records of the Royal Society of London*, 50;2(1996):217-228. ¹⁷¹ Fleming, J. A. "The Thermionic Valve in Wireless Telegraphy and Telephony." *Nature*, 2649;105(1920):716-

^{720,} p. 717.

¹⁷² Fleming, J. A. "The Thermionic Valve in Wireless Telegraphy and Telephony." *Nature*, 2649;105(1920):716-720.

¹⁷³ Adrian, E. D., and Keith Lucas. "On the Summation of Propagated Disturbances in Nerve and Muscle." *The Journal of Physiology*, 44;1-2(1912):68-124.

theory, outlined in 1914.¹⁷⁴ Detection of electrical pulses—action potentials—produced by sensory neurons of the skin showed that they were consistently the same shape and amplitude, leading to the principle that a nerve fiber either generates an impulse in the form of an action potential or it does not—it is a binary "fire" or no fire; there is no in between.¹⁷⁵

Lucas and Adrian also asked how a second stimulus to a peripheral nerve spaced closely enough in time from a previous stimulus of equal intensity might "summate" to produce a muscular contraction when the first stimulus alone was "inadequate" in eliciting a response. They asked, in other words, how a first stimulus "might facilitate the passage of a nervous impulse which followed it."¹⁷⁶ The idea that the stimulus left a lasting impression, however brief, formed the backbone of the research program aimed at uncovering the mechanism of the nerve's response to the stimulus and which was considered by many researchers as the elemental unit of nervous system functioning.

In the 1920s, Adrian asked how stimulation of "end-organs" (i.e., the skin or muscle) related to nerve discharges. He used a valve amplifier to set up experiments which examined how tension, touch, or pressure of constant intensity applied to muscle effected the electrical responses of nerves directly attached to the end organs. The valve amplifier allowed him to observe miniscule electrical potential changes in nerve, measured by a capillary electrometer. The capillary tube of the electrometer, attached to the nerve with conductive metal wires, reflected the nerve's changing electrical potential as changes in surface tension between mercury

¹⁷⁴ Adrian, Edgar D. "The All-or-None Principle in Nerve." *The Journal of Physiology*, 47;6 (1914):460-474; See also, Lucas, Keith. "Croonian Lecture: The Process of Excitation in Nerve and Muscle." *Proceedings of the Royal Society of London B*, 85;582(1912):495-524; Lucas, Keith. "On the Gradation of Activity in a Skeletal Muscle-Fibre." *The Journal of Physiology*, 33;2 (1905):125-137; Lucas, Keith. "On the Refractory Period of Muscle and Nerve." *The Journal of Physiology*, 39;5 (1909):331-340.

¹⁷⁵ Adrian, E. D. *The Basis of Sensation: The Action of the Sense Organs*. London: Christopher, 1928, pp. 28-29; Kandel, Eric R. *In Search of Memory: The Emergence of a New Science of Mind*. New York: W. W. Norton & Company, 2006, pp. 77-80.

¹⁷⁶ Lucas, Keith. *The Conduction of the Nervous Impulse*. London: Longmans, Green and Co., 1917, p. 60.

and an electrolytic solution contained in the tube. Adrian's recordings revealed that frequency of electrical discharges in single nerve fibers can change over time. The sensory nerve impulses from muscle/skin started off at a higher frequency, but their rate of discharge progressively diminished within a single experimental recording even though the stimulus applied to the muscle/skin remained constant. Adrian showed, in other words, that excitation of nerve progressively decreases even if the stimulus persists.

Furthermore, if pressure on a muscle was increased, the frequency of nerve impulses increased. Adrian's nerve-muscle/skin experiments supported his all-or-none theory: size and shape of the nerve impulse does not change, only frequency and number of fibers in action can be altered by changing the strength or quality of the stimulus.¹⁷⁷ Importantly, Adrian demonstrated a new quantitative basis of nervous behavior—that the effect of a stimulus on nervous excitation depends on the temporal pattern of impulses traveling through the nerve. Increased mechanical pressure on a muscle, for example, led to an increased number of impulses observed during a one second period, providing experimental evidence of the temporal relationship between stimulus strength and nervous activity.

In the late 1920s, the Oxford School of physiology, headed by Sherrington, merged its reflex physiology with studies of nervous transmission in its study of the activity of the central nervous system and its effect on the contraction of muscle. Newly concerned, as Adrian was, with the timing of action potential firing, Sherrington-trained scientists like the New Zealand-born neurologist Derek Denny Brown (1901-1981) and Australian neurophysiologist John Carew Eccles (1903-1997) showed that inhibition slowed the frequency of firing of single motor

¹⁷⁷ Hodgkin, A. L. "Edgar Douglas Adrian, Baron Adrian of Cambridge, 30 November 1889 – 4 August 1977." *Biographical Memoirs of Fellows of the Royal Society*, 25(1979):1-73.

neurons and that an increase in reflex response was due to the faster firing of individual motor neurons and the recruitment of additional motor neurons.¹⁷⁸

Simultaneous to studies of electrical transmission in the nervous system, in the 1920s and 1930s the German physiologist Otto Loewi (1873-1961) and British pharmacologist Henry Dale (1875-1968) set out to understand the role of chemical transmission in the nervous system. Their studies in the vagus nerve (part of the autonomic nervous system) of the frog's heart revealed a chemical compound, acetylcholine, at work as a neurotransmitter across the synapse. Their work initiated a "soup" versus "spark" debate, with the "sparkers" dominating the discourse into midcentury.¹⁷⁹ This famous debate over the existence of chemical transmission in cortical synapses occurred in parallel with the electroconductive investigations described in this chapter and also formed part of the overarching project for understanding where the nervous system gets the energy for transmitting information. The debate reveals the dominance of the electroconductive model of nervous system functionality, which neurophysiologists continued to refine, and points to the multifaceted approaches to interrogating the nervous system and how it functions which are not discussed here.

In the early 1940s, the German-British biophysicist Bernard Katz (1911-2003) and Hungarian-American neurophysiologist Stephen Kuffler (1913-1980) spent the war years working with Eccles in his laboratory in Sydney. Together they entered the "soup" versus "spark" debate by probing whether chemical transmission occurred in the central nervous

¹⁷⁸ Eccles, J. C. "The Last Decade at Oxford 1925-1935." In *Sherrington: His Life and Thought*, by J. C. Eccles and W. C. Gibson, 43-74. New York: Springer, 1979. See also, Creed, Richard Stephen, Denny-Brown, Derek, Eccles, John Carew, Liddell, Edward George Tandy, and Charles Scott Sherrington. *Reflex Activity of the Spinal Cord*. London: Oxford University Press, 1932.

¹⁷⁹ For an in-depth discussion of the controversy between the "soups" versus the "sparks" see, Valenstein, Eliot S. *The War of the Soups and the Sparks: The Discovery of Neurotransmitters and the Dispute Over How Nerves Communicate*. New York: Columbia University Press, 2006. See also, Finger, S. "Otto Loewi and Henry Dale: The Discovery of Neurotransmitters." In *Minds Behind the Brain: A History of the Pioneers and Their Discoveries*, 259-279. Oxford: Oxford University Press, 2004.

system. Eccles showed that the all-or-none nerve impulse was not the only type of electrical signal in the brain; smaller electrical potentials near the synapses between neurons suggested that neurons integrate a number of excitatory and inhibitory synaptic potentials before generating (or not) an action potential, as Sherrington originally suggested nearly four decades prior.¹⁸⁰

Also important in this sea change was the work of British neurophysiologist Paul Fatt (1924-2014) and Katz which showed experimentally that spontaneous quantal release of chemical transmitter from presynaptic terminals of nerve fibers can evoke postsynaptic responses at the muscle end-plate (where a motoneuron meets a muscle) which are below the action potential threshold; the observed end-plate potential proved there could be a post-synaptic change in membrane potential that is *not* a result of action potential firing.¹⁸¹ Previous to these conclusive experiments, Katz and others who had observed subthreshold local responses often explained them away, for example by assuming that a sufficient length of the nerve axon had to be stimulated in order to generate an action potential.¹⁸²

Concern with the timing of nervous conduction and its role in functionality, however, remained at the heart of neurophysiological inquiry in the first half of the twentieth century. In 1907 Lucas remarked that physiologists had recently "become more fully aware of the part which the duration of the exciting current plays in the production of an excitation."¹⁸³ Through

¹⁸⁰ Eccles trained with Sherrington and they collaborated on several papers together, primarily regarding inhibition in the central nervous system. For a description of Eccles contribution to revealing the existence of synaptic potentials, see Kandel, Eric R. *In Search of Memory: The Emergence of a New Science of Mind*. New York: W. W. Norton & Company, 2006, pp. 90-102.

¹⁸¹ Fatt, Paul and Bernard Katz. "An Analysis of the End-Plate Potential Recorded with an Intracellular Electrode." *The Journal of Physiology*, 115;3(1951):320-370; Fatt, Paul and Bernard Katz. "Spontaneous Subthreshold Activity at Motor Nerve Endings." *The Journal of Physiology*, 117;1(1952):109-128.

¹⁸² See e.g., Katz, Bernhard. "Experimental Evidence for a Non-Conducted Response of Nerve to Subthreshold Stimulation." *Proceedings of the Royal Society B*, 124;835(1937):244-276.

¹⁸³ Lucas, Keith. "On the Rate of Variation of the Excitation Current as a Factor of Electric Excitation." *The Journal of Physiology*, 36;4-5(1907):253-274, p. 270. On p. 253, Lucas stated that du Bois-Reymond attempted a similar experiment in 1862, "but was baulked by the inadequacy of his apparatus."

several experiments before his death while serving the British Army in World War I, Lucas sought to elucidate how timing of a stimulus affects muscular contraction. By graphing changes in the minimum threshold needed to elicit a "propagated disturbance" in relation to changes in stimulus strength and duration, Lucas observed "excitable substances" near the space where nerve fibers and muscle fibers meet which possessed a *different* minimal threshold to produce muscular contraction than the nerve fiber, and which depended on the duration of application of the electric stimulus.¹⁸⁴

This finding provided early evidence in favor of chemical transmission in the nervous system, which could help explain the differing responses to duration of stimulation.¹⁸⁵ In his posthumously-published monograph, Lucas described the "central problem of our inquiry" with regard to understanding nervous conduction as determining how the nervous impulse can be "modified by various conditions"; of importance was the "antecedent history of the impulse" as well as "the momentary condition of the nerve."¹⁸⁶ Timing mattered, in other words, and paying attention to the temporal properties of nervous conduction would help to uncover its mechanism. Attention to temporal relations suggests that neurophysiologists presumed the nervous system had a way of delineating current states from previous ones and consequently that future states might be altered as well.

In 1911, Lucas attempted to explain a physiological anomaly—the phenomenon of Wedensky inhibition—in terms of timing of stimuli relative to their occurrence during a nerve fiber's relative refractory period (the brief period of time immediately after a nervous discharge

¹⁸⁴ Lucas, Keith. "The Excitable Substances of Amphibian Muscle." *The Journal of Physiology*, 36;2-3(1907):113-135.

¹⁸⁵ Lucas, Keith. "The Excitable Substances of Amphibian Muscle." *The Journal of Physiology*, 36;2-3(1907):113-135.

¹⁸⁶ Lucas, Keith. *The Conduction of the Nervous Impulse*. London: Longmans, Green and Co., 1917, p. 9.

in which a fiber cannot produce a second discharge). Over a quarter century prior, in 1885, the Russian physiologist Nikolai Wedensky (1852-1922) observed what seemed like a paradox while experimenting with a nerve-muscle preparation: strong or rapidly recurring electric stimuli to a nerve fiber produced a small muscle contraction whereas weak or slowly recurring stimuli produced a continued tetanus (i.e., sustained contraction) of the muscle.

Lucas and others engaged in various experiments to understand the refractory period as a key to understanding the mechanism of nervous conduction. Although experimenters could easily detect muscular fatigue by observing a decrease in the tonus or strength of contraction, there existed no visible marker of a nerve's energy stores, and most thought the nerve to be indefatigable. The refractory period challenged the indefatigability notion of nerve and raised questions about the amount of energy a nerve can liberate per unit time of activity.¹⁸⁷ Experiments exploring the nerve's refractory period and fatigability reflected concerns and unanswered questions about how the nerve produces and uses limited stores of energy during a period of excitation.

In addition to electrophysiological approaches, other methodological searches for explanations of nerve conduction centered around asking how nerves got the energy to produce its electrical discharge. Research on heat production in nerve and crossover work with respiratory physiology suggests other attempts to explain electrical conductance in nerve as part of ongoing discourse about energy conservation in biological organisms. The venture spearheaded by the British physiologist A. V. Hill (1886-1977) reveals a shared project and intense interest in uncovering clues about what supplies the energy for nervous conduction. Hill, who won the 1922 Nobel Prize for measuring heat production in muscle, described a parallel

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¹⁸⁷ Gerard, Ralph. "The Activity of Nerve." *Science*, 66;1717(1927):495-499.

search for heat production in nerve occurred "in order to settle the question of whether the nerve impulse is the sort of physical wave in which the whole of the energy for transmission is impressed on the system at the start."¹⁸⁸ According to Hill, observations of the nerve's "infatigability" supported the notion that the nerve impulse supplied sufficient energy for nervous activity, whereas the existence of an absolute refractory period suggested that the nerve impulse "is unlike any physical wave in which the energy is supplied at the start."¹⁸⁹ Although measurement of nervous heat production during nervous impulse transmission did not provide answers to how nerves generate and propagate electrical activity, Hill's experiments make clear the physiological imperative for interrogating energy loss in biological tissue as a necessary component toward understanding nervous system functionality.

Married French neurophysiologists Louis Lapicque (1866-1952) and Marcelle Lapicque (1873-1960) had a theory of the relationship between time and nervous conduction which did not hold a place for Lucas' "excitable substances," to the ire of some of Lucas' supporters, especially the British physiologist William Rushton (1901-1980), who participated in a several-year debate over the issue with Louis through sparring publications in *The Journal of Physiology*.¹⁹⁰ Louis was a professor at the Muséum d'Histoire Naturelle and later at the Sorbonne, yet despite their more than forty-year collaboration and Louis' declaration that Marcelle contributed equally to their research, Marcelle did not receive equal credit. Moreover, she held no formal position other than associate director and, after her husband's death, as director of the physiology laboratory

¹⁸⁸ Hill, A. V. "The Heat Production of Muscle and Nerve, 1848-1914: The First Chapter of a Future Monograph." *Annual Reviews of Physiology*, 21(1959):1-19, p. 16.

¹⁸⁹ Hill, A. V. "The Heat Production of Muscle and Nerve, 1848-1914: The First Chapter of a Future Monograph." *Annual Reviews of Physiology*, 21(1959):1-19, p. 16.

¹⁹⁰ See e.g., Rushton, W. A. H. "Lapicque's Theory of Curarization." *The Journal of Physiology*, 77;4(1933):337-364.

they worked in together. Marcelle's name did not appear in Lapicque's entry in the *Dictionary of Scientific Biography* written by his student in the 1970s.¹⁹¹

In 1926, Stemming from experimental work as far back as 1907, Louis Lapicque presented the chronological theory of isochronism to explain excitation and inhibition. The theory posited that two physiological elements must be chronologically tuned (to have isochronism) in order for excitement to be transmitted from one physiological element to another. He used the term *chronaxie* as a measure of the influence of time in excitation; he defined chronaxie as the physiological time constant of a cell. If a nerve and a muscle have similar chronaxies, said Lapicque, the nerve could excite the muscle, but not if their chronaxies differed. Isochronism permitted excitation while heterochronism prohibited it. Thus, for Lapicque inhibition was the absence, or the canceling out, of excitation, and depended on the time constants of nerve and muscle, not on "excitable substances."

In recounting the "interesting and amiable controversy" between Lapicque and Rushton to the 14th International Physiological Congress in 1932, A. V. Hill noted the importance of the consideration of time in living functions. Hill said: "In different muscles, or different nerves, different properties appear: but adjust the scale of time for each and many of their properties become strikingly similar. It is not in excitation alone, but in many other functions, that a «chronaxie» ; a «time scale» exists." True to form as a mechanistic materialist, Hill said that time scale "cannot depend on visible structure" but instead "must depend on differences of molecular

¹⁹¹ Ogilvie, Marilyn, and Joy Harvey (eds.). *The Biographical Dictionary of Women in Science: Pioneering Lives from Ancient Times to the Mid-20th Century, Vol. 2, L-Z.* New York: Routledge, 2000; pp. 745-746; Lykknes, Annette, Opitz, Donald L., and Brigitte Van Tiggelen (eds.). *For Better or For Worse? Collaborative Couples in the Sciences.* Science Networks Historical Studies, Vol. 44. New York: Springer, 2012, pp. 66-67.

structure or molecular organization—we look to physical and organic chemistry for an indication of their nature."¹⁹²

The drug curare, and other substances like alcohol, Lapicque said, can change the chronaxies of muscles and/or nerve fibers, ceasing excitation. So, too, can their subordination to higher nervous centers. The changed time constant, as a property of the nerve fiber or muscle affecting nervous conduction, is a representation of its current state, different from its previous one. Although Lapicque was unaware of Wedensky's work when proposing his theory, he later noted in his 1935 closing address to the 15th International Physiological Congress that Wedensky's concept of lability related to chronaxie.

In 1935, the Russian physiologist Alexei Oukhtomsky (1875-1942), a self-proclaimed member of Wedensky's St. Petersburg school of physiology, articulated Wedensky's lability as a function of a physiological substrates' ability to change its degree of isochronism; lability implied the capacity of nervous tissue to modify its functioning. Acceptance of this concept requires that nerves account for a history of events, said Oukhtomsky, and allows for adaptability and possible training of a system. Oukhtomsky said it was time for physiologists to catch up with modern physics and its consideration of problems of time and the history of events. Oukhtomsky was inspired by French mathematician Emil Picard's (1856-1941) principle of non-heredity, which states that if forces depend on their movement in time, we must consider the future of a system as depending not just on its present state, but also on the immediately previous one.¹⁹³

¹⁹² Hill, A. V. "Energy Exchanges in Muscle and Nerve: Myothermic and Nevrothermic Experiments." *Archivo di Scienze Biologiche, XIV Congreso Internazionale di Fisiologa Conferenze e Sunti Delle Comunicazioni*, 18;1-2-3-4(1933):3-14, p. 10.

¹⁹³ Oukhtomsky, A. A. "La Labilité Physiologique et L'Acte D'Inhibition." In *Proceedings of the XVth International Physiological Congress. Leningrad-Moscow, August 9thto 16th, 1935. The Sechenov Journal of Physiology of the USSR, Vol. XXI, No. 5-6. Edited by S. M. Dionessov, A. V. Eisenberg, and L. N. Fedorov, 611-615. Moscow-Leningrad: State Biological and Medical Press, 1938.*

The seeming incongruity of Wedensky inhibition factored into several theories to explain the mechanism of nervous conduction. Lucas and Adrian explained Wedensky inhibition as depending on when a stimulus landed within a nerve's relative refractory period. Lapicque's chronological theory of isochronism, which centered around measurement and comparison of chronaxies, or mathematical time constants, of nerves and muscles, became quite influential. A 1935 paper in the *Psychological Bulletin* declared there to be 1,000 to 1,200 studies on the subject of chronaxie, most published since 1925.¹⁹⁴

Studies showed that many factors, including drugs (besides curare), temperature, and muscle tension, for example, could alter chronaxies, effecting whether a nervous impulse might be conducted. Other studies delved deeper into the effects of various drugs on the modification of chronaxie, contributing to evidence for chemical transmission. One psychologist declared that chronaxic methods could help provide answers in the field of integration, elucidating how learning a motor skill brings about isochronism between nerve and muscle through repetition of stimulation.¹⁹⁵ Lapicque and Lapicque also conducted experiments to show how cells from the brain could modify chronaxies in the periphery, theorizing "higher level" control over peripheral action. In 1935, Louis Lapicque declared he was applying chronaxic methods to study Pavlovian conditioned reflexes.¹⁹⁶

The phenomenon of Wedensky inhibition prompted researchers to consider yet another relationship between nervous conduction and time. Wedensky inhibition, "the curious fact that activity can induce inactivity," presented a challenge which drove of a group of

¹⁹⁴ Wilson, M. O. "Chronaxie." Psychological Bulletin, 32;1(1935):4-32.

¹⁹⁵ Wilson, M. O. "Chronaxie." Psychological Bulletin, 32;1(1935):4-32.

¹⁹⁶ Lapicque, L. "Concluding Plenary Session: Quelques Progrès Récents dans la Connaissance du Mécanisme Nerveux." In *Proceedings of the XVth International Physiological Congress. Leningrad-Moscow, August 9thto 16th, 1935. The Sechenov Journal of Physiology of the USSR*, Vol. XXI, No. 5-6. Edited by S. M. Dionessov, A. V. Eisenberg, and L. N. Fedorov, 601-610. Moscow-Leningrad: State Biological and Medical Press, 1938.

neurophysiologists from Europe, Japan, Russia, and the U.S. towards a search to explain its mechanism.¹⁹⁷ The phenomenon was puzzling—how could a series of experimentally-delivered *fast* or *strong* electric stimuli to nerves produce little or no muscle contraction while a series of *weak* or *slowly recurring* stimuli leads to sustained contraction? New questions about the relationship between stimulus duration and intensity had researchers asking—how does timing of the stimulus play into nervous conduction? How does a cell's previous history affect its present output?

Wedensky's inhibition shaped the Nobel Prize-winning Russian physiologist Ivan Pavlov's (1849-1936) ideas about higher nervous activity in the cerebral cortex.¹⁹⁸ The factor of time featured prominently in Pavlov's work on conditioned salivary reflexes in dogs and shaped the work of many neurophysiologists attempting to understand the biological basis of adaptation and learning. Pavlov's work showed that a conditioned stimulus will only produce an effect if it is associated in time with an innate unconditioned stimulus. Through inhibitory processes which operate in the central nervous system, said Pavlov, reflexes can be trained and perfected thanks to the lability (probably no coincidence he used Wedensky's term) of the processes in them.

After midcentury, neurophysiologists began using Pavlov's theory of conditioned reflexes to design experiments with the specific goal of understanding the cellular basis of learning and memory in the nervous system. Austrian-American neuroscientist Eric Kandel (1929-), who won the Nobel Prize in 2004 for his work eliciting conditioned reflexes in the

¹⁹⁷ Cannon, W. B. "Some Implications of the Evidence for Chemical Transmission of Nerve Impulses." In *Proceedings of the XVth International Physiological Congress. Leningrad-Moscow, August 9thto 16th, 1935. The Sechenov Journal of Physiology of the USSR, Vol. XXI, No. 5-6. Edited by S. M. Dionessov, A. V. Eisenberg, and L. N. Fedorov, 13-23. Moscow-Leningrad: State Biological and Medical Press, 1938, p. 19.*

¹⁹⁸ Brazier, Mary A. B. (editor). *The Central Nervous System and Behavior. Transactions of the First Conference – February 23, 24, 25, and 26, 1958.* Madison, NJ: Madison Printing Co., Inc., 1959, p. 96.

cephalopod *Aplysia*, stated in his memoir he "decided to try to simulate in the nerve cells of *Aplysia* the patterns of sensory stimulation that Pavlov had used in his learning experiments."¹⁹⁹

Consideration of the temporal component of nervous conduction and transmission by early twentieth-century neurophysiologists formed an integral part of the shared project to understand the mechanism of nervous conduction and its relation to excitation. Experiments involving different stimulus frequencies and durations and observations of the refractory period, fatigue, summation, Wedensky inhibition, and conditioning all indicated investigators' ability to measure and compare different states of the nerve. The temporality of nervous function meant it was capable of change, and that organic change was associated with electroconductive change. Concern with temporality and its relationship to organic change can be understood in light of the Sherringtonian imperative to uncover how the nervous system integrates neuronal activity in order to assemble complex reflex patterns that contribute to the behavior of a unified individual organism whose ultimate task is to better dominate its environment.

The membrane and the action potential

The German chemist Walter Nernst (1864-1941), trained as a physicist in Berlin, helped usher in the "new" physical chemistry at the turn of the century, eventually winning the Nobel Prize in 1920 for his success at bridging the molecular conception of chemistry with thermodynamics. Nernst's equations, derived from Helmholtz's, provided an interpretive framework for explaining physicochemical phenomena in terms of electrolytic dissociations and energy transformations.²⁰⁰ A. V. Hill's 1932 *Chemical Wave Transmission in Nerve* (delivered that year as a lecture at Christ's College, Cambridge), following from the Nernstian agenda,

¹⁹⁹ Kandel, Eric C. *In Search of Memory: The Emergence of a New Science of Mind.* New York: W. W. Norton & Company, 2006, p. 159.

²⁰⁰ J. R. P. "Prof. Walter Nernst, For. Mem. R.S." *Nature*, 149;3779(1942):375-376.

called on physical chemists to help provide a mechanistic understanding of the nerve impulse. Hill considered the nerve impulse as a message, or an event – not a substance or a form of energy – which formed the basis of nerve activity, but noted that an "electric change seems to be a universal accompaniment of the impulse, it can be used as a sign of its presence, as a measure of its size."²⁰¹

Hill was convinced of the direct relationship between nervous electric excitation and the membrane potential of neurons. Uncovering this relationship, believed Hill, would help to explain the fundamental nature of nervous system functioning. "The problem, above all others," was, he said: "How can a rapid cycle of rise and fall of electrical conductivity follow an electrical discharge through a film? [i.e., a membrane]; this problem, he said "is perhaps the hardest and most fundamental. Its answer will go far to explain electric excitation, and therewith the mechanism of propagation of the nervous impulse."²⁰²

Although experimenters could measure potential differences across recording electrodes when observing nervous activity thanks to improvements in technique by Adrian and others, the origin of these electrical potentials remained in question. Hill cited Nernst's 1908 theory which postulated that electric current could be induced by a change in the number of ions across a membrane as well as the American botanist Winthrop John Van Leuven Osterhout's (1894-1961) 1931 theory positing discharge through a dielectric surface (i.e., a polarized insulating material) as two likely explanations.²⁰³ Hill went on to cite the ample evidence for the direct relationship between the mechanism of conduction of the nervous impulse with the electric current observed by experimenters, including that "[t]he impulse and its electrical accompaniment travel with the

²⁰¹ Hill, A. V. Chemical Wave Transmission. London: Cambridge University Press, 1932, p. 8.

²⁰² Hill, A. V. Chemical Wave Transmission. London: Cambridge University Press, 1932, p. 47.

²⁰³ Hill, A. V. Chemical Wave Transmission. London: Cambridge University Press, 1932, p. 29.

same speed and have many common properties" and "[t]he voltage and duration of the action current are such as will in fact excite."²⁰⁴ For all intents and purposes, the observed electrical current *was* the impulse.

Hill, Sherrington, and Adrian's younger colleagues, English neurophysiologists Alan Lloyd Hodgkin (1914-1998) and Andrew Fielding Huxley (1917-2012), Bernard Katz, Paul Fatt, American biophysicist Kenneth S. Cole (1900-1984), American biologist Howard J. Curtis (1906-1972), and a new generation of neurophysiologists, following from the imperative for understanding the nature of electric excitation, combined results from nerve-muscle experiments with axonology with the goal of uncovering the mechanism of nervous conduction. Axonology was spurned by the introduction of the squid giant axon into neurophysiological research which allowed scientists to record electrical potentials from a single, large-diameter axon and was later further bolstered by a new technique which allowed for recording from the inside of the fiber. Axonology focused on the electrical properties of nerve fiber conduction itself, without its connection to muscle. Experiments conducted in invertebrates on the isolated nerve fiber produced no functional output (in the form of muscle contraction, for example), but because of the similar electrical properties of invertebrate and vertebrate nerves, they were understood to be analogous to experiments in nerve-muscle preparations which were performed using vertebrate tissue.

Hodgkin and Katz, reflecting on their careers in 1976 and 1985 respectively (long after they had both won their Nobel Prizes), cited Hill's 1932 lecture as directly influencing their ideas and experimental designs.²⁰⁵ In the mid-1930s, however, not everyone was so convinced by

²⁰⁴ Hill, A. V. Chemical Wave Transmission. London: Cambridge University Press, 1932, p. 38.

²⁰⁵ Hodgkin, A. L. "Chance and Design in Electrophysiology: An Informal Account of Certain Experiments on Nerve Carried Out Between 1934 and 1952." *The Journal of Physiology*, 263;1(1976):1-22; Katz, Bernard.

Hill's speculations. Hodgkin sought to settle the controversy over the mechanism of nervous conduction with physiologists at the University of Washington in St. Louis, including the Americans Joseph Erlanger (1874-1965), Herbert Spencer Gasser (1888-1963), Francis O. Schmitt (1903-1995), and the Spaniard Rafael Lorente de Nó (1902-1990), who were skeptical about the local circuit theory and membrane theory to explain electrical excitability in nerve cells. The single cell electrical recording experiments described in Erlanger and Gasser's influential 1937 *Electrical Signs of Nervous Activity* reflected their disbelief that the membrane potential was directly related to the process of excitation.

Hodgkin helped persuade Erlanger that the nerve fiber acts like a local circuit by setting up an experiment which compared the conduction velocity of an electrical impulse when a crab nerve was submerged in oil (a high external resistance) versus when it was submerged in sea water (a low external resistance). The fiber conducted faster in the sea water, consistent with the idea that the local circuit of the fiber depends on the external medium.²⁰⁶ In 1874, the German physiologist Ludimar Hermann (1838-1914), student of du Bois-Reymond, proposed the local circuit theory to explain how the rise in electrical potential in a nerve fiber propagates along its length. Hermann conceived of the nerve fiber as having an internal fluid compartment which is separated from an external fluid by an insulating material. Hermann said the rise in local potential of a particular region of the nerve fiber makes the external fluid negative in

[&]quot;Bayliss-Starling Memorial Lecture (1985): Reminiscences of a Physiologist, 50 Years After." *The Journal of Physiology*, 370(1986):1-12.

²⁰⁶ Katz, Bernard. "Sir Bernard Katz." In *The History of Neuroscience in Autobiography*, Vol 1. Edited by Larry R. Squire, 348-381. Washington, DC: Society for Neuroscience, 1996; Hodgkin, A. L. "Chance and Design in Electrophysiology: An Informal Account of Certain Experiments on Nerve Carried Out Between 1934 and 1952." *The Journal of Physiology*, 263;1(1976):1-22.

comparison, stimulating nearby areas of the nerve and thereby propagating the electrical signal along the length of the fiber.²⁰⁷

Although Hodgkin's work convinced some physiologists that the nerve acts as part of a local circuit—that the external *and* internal fluid contributes to a nerve conducting electricity, it still did not explain *how*, exactly, nerve fibers conduct electricity. The German physiologist Julius Bernstein's (1839-1917) membrane theory, posited in 1902, provided a possible answer. Bernstein maintained that charged ions flow across membranes and generate electrical potential differences across an ion-selective membrane.²⁰⁸ Determined to uncover the mechanism of nervous conduction with valve amplification and cathode-ray oscillography technology at their disposal, neurophysiologists of the 1930s relied on the membrane theory when designing experiments which would record electrical changes in nerve fibers.²⁰⁹

The membrane theory postulated that potassium was responsible for carrying most of the electrical current during an action potential and that the membrane was somehow permeable to potassium.²¹⁰ By the 1940s, Cole, Hodgkin, Huxley, and a large group of researchers had rallied around cable theory, a mathematical combination of local circuit-theory with membrane theory which modified Nernst's equations for ion flow to help explain nerve electrical conduction. Nernst, Bernstein (who trained with du Bois-Reymond and later worked with Helmholtz) and

 ²⁰⁷ Turkel, William J. "Discovering Electric Worlds." In *Spark from the Deep: How Shocking Experiments with Strongly Electric Fish Powered Scientific Discovery*, 178-205. Baltimore: Johns Hopkins University Press, 2013.
 ²⁰⁸ Seyfarth, Ernst-August. "Julius Bernstein (1839-1917): Pioneer Neurobiologist and Biophysicist." *Biological Cybernetics*, 94(2006):2-8.

²⁰⁹ Ludimar Hermann's local circuit theory (1874) posited that electrical current spread along a nerve fiber in a cable-like manner but raised the question of how current did not dissipate along the length of the fiber. Experiments from 1925 supported saltatory conduction (i.e., that current is boosted at nodes, providing enough current to diffuse, or "jump" to the next node, where it was boosted again). See e.g., Turkel, William J. "Discovering Electric Worlds." In *Spark from the Deep: How Shocking Experiments with Strongly Electric Fish Powered Scientific Discovery*, 178-205. Baltimore: Johns Hopkins University Press, 2013.

²¹⁰ See e.g., Hodgkin, A. L. "The Effect of Potassium on the Surface Membrane of an Isolated Axon." *The Journal of Physiology*, 106(1947):319-340.

Osterhout's ideas about ions moving across biological membranes spoke to the question of where the nerve gets energy to produce its functional activity.²¹¹ Cable theory, therefore, must be understood as an outgrowth of the second half of the nineteenth-century attempts to explain biological phenomena in physico-chemical terms and the laws of thermodynamics.

Experimenters relied on cable theory when designing experiments; work around cable theory involved experiments to understand, for example, how membrane resistance contributed to a nerve fiber's electrical conductance. Scientists used a variety of experimental designs, techniques, and tools to figure out how ions flow across the cell membrane to produce electrical potential. They could dip an axon in oil (to keep ions in a thin film of sea water close to the fiber membrane, facilitating passage into or out of the membrane) or change the concentrations of ions in the artificial solution made to mimic extracellular fluid, for example, and record how different ionic concentrations affected membrane conductance.²¹² In an October 17, 1946 letter from Hodgkin to Cole, Hodgkin said he and Huxley "feel pretty certain" that the conductance changes they reported in a recent letter to *Nature* "are due to potassium leakage…I have become very interested in the mechanism by which an axon absorbs K [potassium] against a concentration gradient…and we feel pretty sure that there is some active process at work. The most likely type of mechanism seems to me to be an active intrusion of Sodium, but for this I have no real

²¹¹ On Bernstein, see Seyfarth, Ernst-August. "Julius Bernstein (1839-1917): Pioneer Neurobiologist and Biophysicist." *Biological Cybernetics*, 94(2006):2-8.

²¹² Huxley, A. F. "Electrical Activity in Nerve: The Background up to 1952." In *The Axon: Structure, Function and Pathophysiology*. Edited by S. G. Waxman, J. D. Kocsis, and P. K. Stys, 3-10. New York: Oxford University Press, 1995; Schuetze, S. M. "The Discovery of the Action Potential." *Trends in Neuroscience*, 6(1983):164-168; Hodgkin, A. L., and A. F. Huxley. "Action Potentials Recorded from Inside a Nerve Fibre." *Nature*, 144(1939):710-711. See also, Hodgkin, A. L. *Chance and Design: Reminiscences of Science in Peace and War*. Cambridge: Cambridge University Press, 1992; Hodgkin, A. L. *The Conduction of the Nervous Impulse*. Liverpool: Liverpool University Press, 1967; Katz, Bernard. *Nerve, Muscle, and Synapse*. New York: McGraw-Hill, 1966.

evidence."²¹³ Evidence that potassium moves across the membrane against its concentration gradient prompted Hodgkin to consider the active processes going on at the molecular level.

A 1949 paper by Hodgkin and Katz further supported the idea of active processes occurring at the membrane. Using internal electrodes to measure the internal membrane potential of the squid giant axon, the pair observed an apparent reversal in membrane potential during the action potential which could not be explained by membrane theory. Instead of rejecting membrane theory, Hodgkin and Katz used the mathematical equations which underpinned the theory to conclude that "a large reversal of membrane potential can be obtained if it is assumed that the active membrane" becomes "highly and specifically permeable to sodium."²¹⁴ The sodium hypothesis was quickly incorporated into the imminent Hodgkin-Huxley model of axon action potential initiation and propagation.

During the now forgotten "battle of the sheath" controversy, Lorente de Nó, former student of famed neuroanatomist Ramón y Cajal, challenged Hodgkin and other axonologists who believed the epineurium, a connective tissue surrounding peripheral nerve fibres, was impermeable to ions and acted as an insulator of electric current.²¹⁵ Skeptical of local circuit theory and membrane theory, Lorente de Nó mounted arguments against the role of the epineurium using both electrophysiological and histological evidence.²¹⁶ Physiologists responded

²¹³ Alan L. Hodgkin to Kenneth S. Cole, October 17, 1946, D.96, Hodgkin papers, Trinity College Archive, University of Cambridge, Cambridge, England; See also, Hodgkin, A. L., and A. F. Huxley. "Potassium Leakage from an Active Nerve Fibre." *Nature*, 158(1946):376-377.

²¹⁴ Hodgkin, A. L., and B. Katz. "The Effect of Sodium Ions on the Electrical Activity of Giant Axon of the Squid." *The Journal of Physiology*, 108(1949):37-77, p. 38.

²¹⁵ It is now understood that the axon membrane itself has channels which allows flow of ions between the intracellular and extracellular fluid and the myelin provides insulation.

²¹⁶ Lorente de Nó, Rafael. "Observations on the Properties of the Epineurium of the Frog Nerve." *Cold Spring Harbor Symposium on Quantitative Biology – The Neuron*, 17(1952):299-315.

to Lorente de Nó's challenge by attending to nerve anatomy when "stripping" nerve of its epineurium and examining its physiological effects.²¹⁷

Lorente de Nó also challenged the concept of saltatory conduction, suggested by the Canadian-American biologist Ralph Lillie (1875-1952) in 1925 as a way for the nerve to save energy during conduction by facilitating "jumping" of the electrical impulse from one node to another along a nerve's axon. Working under the assumptions of local circuit theory, Lillie observed faster electrical conduction along an iron wire by surrounding the wire with an insulating glass tube with spaced holes (nodes). Lillie's results prompted him to speculate on analogous structures in living organisms, but their presence was difficult to determine experimentally.²¹⁸ Electrophysiological experiments in which specific lengths of nerve fibre were narcotized or exposed to cold to prevent electrical conductance in a small area tested and, in some cases, supported (and in others, undermined) the theory of the "jumping" nerve impulse along the axon.²¹⁹ By the late 1940s, there was considerable electrophysiological evidence for saltatory conduction in peripheral nerves at the nodes of Ranvier, the spaces between the insulating layer of myelin surrounding some axons.²²⁰ In a 1948 letter to Hodgkin, however, Lorente de Nó claimed nerve fibres in the central nervous system do not have nodes of Ranvier;

²¹⁷ See e.g., Rashbass, C., and W. A. H. Rushton. "The Relation of Structure to the Spread of Excitation in the Frog's Sciatic Trunk." *The Journal of Physiology*, 110(1949):110-135.

²¹⁸ Lillie, R. S. "Factors Affecting Transmission and Recovery in the Passive Iron Nerve Model." *Journal of General Physiology*, 7;4(1925):473-507.

²¹⁹ See e.g., Kato, G. *The Theory of Decrementless Conduction in Narcotised Region of Nerve*. Tokyo: Nankōdō, Hongo, 1924; Kato, G. "On the Excitation, Conduction, and Narcotisation of Single Nerve Fibres." *Cold Spring Harbor Symposium on Quantitative Biology – Excitation Phenomena*, 4(1936):202-213; Hodgkin, A. L. "Evidence for Electrical Transmission in Nerve." *The Journal of Physiology*, 90;2(1937):183-210; Tasaki, I. "The Strength-Duration Relation of the Normal, Polarized and Narcotized Nerve Fiber." *American Journal of Physiology*, 125;2(1939):367-379; Tasaki, I. "Electric Stimulation and the Excitatory Process in the Nerve Fiber." *American Journal of Physiology*, 125;2(1939):380-395.

²²⁰ See e.g., Huxley, A. F. and R. Stämpfli. "Evidence for Saltatory Conduction in Peripheral Myelinated Nerve Fibres." *The Journal of Physiology*, 108;3(1949):315-339; Frankenhaeuser, B. "Saltatory Conduction in Myelinated Nerve Fibres." *The Journal of Physiology*, 118;1(1952):107-112; Frankenhaeuser, B. and Dietrich Schneider. "Some Electrophysiological Observations on Isolated Single Myelinated Nerve Fibres (Saltatory Conduction)." *The Journal of Physiology*, 115(1951):177-184.

they have continuous myelin coverings and only breaks in myelin at particular points, he said, "anatomical facts" which challenged the idea of saltatory conduction occurring in the brain.²²¹

Unresolved questions around nerve membrane permeability to ions prompted neurophysiologists at midcentury to more deeply consider the molecular structure of nerve cells using the emerging tools of molecular biology. The experimental observation of hyperpolarization (the membrane potential becoming more negative with respect to its resting potential, further from the threshold needed to generate an action potential) following an impulse which is dependent on potassium concentration baffled scientists trying to hypothesize on its mechanism. According to Nernst's equations, the extracellular potassium concentration after an impulse is too low to account for the observed hyperpolarizing effect, prompting scientists to consider a second diffusion barrier between the excitable nerve membrane and the extracellular space which keeps the potassium concentration high just across the membrane. Scientists looked to electron microscopy studies for an anatomical clue—they saw the potential for a small aqueous space between Schwann cells surrounding axons which might trap potassium ions near the outside of the axon membrane. Another line of evidence using metabolic inhibitors, however, showed that the hyperpolarization could be dependent on oxidative metabolism. The work with metabolic inhibitors suggested the presence of structural channels allowing ion flow which are actively controlled through biochemical mechanisms (i.e., using chemical energy to direct ions through channels). Either way, biophysicists at midcentury needed the help of anatomists and biochemists to help explain hyperpolarization.²²²

²²¹ Rafael Lorente de Nó to Alan L. Hodgkin, January 9, 1948, H.9, Hodgkin papers, Trinity College Archive, University of Cambridge, Cambridge, England.

²²² See e.g., Frankenhaeuser, B. and A. L. Hodgkin. "The After-Effects of Impulses in the Giant Nerve Fibres of Loligo." *The Journal of Physiology*, 131(1956):341-376; Hodgkin, A. L. "The Croonian Lecture - Ionic Movements and Electrical Activity in Giant Nerve Fibres." *Proceedings of the Royal Society of London B*, 148;930(1958):1-37.

In 1952, Hodgkin and Huxley released their famous model derived from cable theory explaining the ionic mechanisms underlying the action potential. Their series of five papers used the voltage clamp method in order to measure ionic currents across the axon membrane (previously they could only measure voltage change).²²³ To "clamp" voltage, a feedback amplifier applied the current necessary to keep a constant voltage, or membrane potential; the current applied by the amplifier is understood to be equal and opposite to the flow of current through a defined area of the squid giant axon membrane.²²⁴ Hodgkin and Huxley changed the sodium concentration in the fluid medium in which the axon was submerged and measured the "behaviour of the axon" (i.e., the changes in membrane current) in response to short electric current shocks at various "clamped" voltages.²²⁵ Hodgkin and Huxley fit their experimental data curves to nonlinear differential equations which could explain how ionic flow across a nerve membrane created an action potential. Having figured this out, however, the active process underlying membrane permeability remained undiscovered, and a new set of research questions would soon catch neurophysiologists' attention.

²²³ Hodgkin, A. L., Huxley, A. F., and B. Katz. "Measurement of Current-Voltage Relations in the Membrane of the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):424-448; Hodgkin, A. L., and A. F. Huxley. "Currents Carried by Sodium and Potassium Ions Through the Membrane of the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952): 449-472; Hodgkin, A. L., and A. F. Huxley. "The Components of Membrane Conductance in the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):473-496; Hodgkin, A. L., and A. F. Huxley. "The Dual Effect of Membrane Potential on Sodium Conductance in the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):497-506; Hodgkin, A. L., and A. F. Huxley. "A Quantitative Description of Membrane Current and its Application to Conduction and Excitation in Nerve." *The Journal of Physiology*, 117(1952):500-544.

²²⁴ Cole and his collaborator at Woods Hole, George Marmont, were the first to work with a feedback amplifier in the single squid giant axon. Their 1947 experiments were published in a 1949 paper by Marmont. In that paper, Marmont directed interested readers to a book on feedback theory by H. W. Bode, *Network Analysis and Feedback Amplifier Design*, New York: Nostrand, 1945. In the preface to the 1945 book, Bode stated he compiled the notes for the book in 1938 and 1939 for a course which primarily discussed amplifiers "used as repeaters in long distance telephone systems" (p. iv), but the book wound up becoming "a treatise on general network theory" (p. iii). Marmont, M. "Studies on the Axon Membrane – I. A New Method." *Journal of Cellular and Comparative Physiology*, 34;3(1949):351-382; For more on the Marmont paper as the only full account of the Cole and Marmont 1947 experiments, see Huxley, A. F. "Kenneth Stewart Cole." *Biographical Memoirs, Vol. 70*, 24-46. Washington, DC: The National Academies Press, 1996.

²²⁵ Hodgkin, A. L., Huxley, A. F., and B. Katz. "Measurement of Current-Voltage Relations in the Membrane of the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):424-448; p. 432.

Although Hodgkin and Huxley's mathematical model of ion exchange during action potential generation was a near-instant success, they could not explain the precise molecular mechanism which allowed for ions to move across the membrane. Their final 1952 paper hypothesized that a "lipoid soluble carrier which bears a large negative charge" took a sodium ion with it across the lipid membrane.²²⁶ In the first of their 1952 series of papers, the authors explained their experimental set-up as including Perspex (like plexiglass) barriers sealed with Vaseline around the squid giant axon which ensured current flowed down an electrically-isolated channel created between two Perspex barriers.²²⁷ Hodgkin and Huxley did not refer to the possible existence of structural channels in the membrane in 1952, but they did refer to studies from the past few years using radioactive tracers which evidenced the movements of potassium and sodium ions across the membrane. By his 1957 Croonian Lecture, however, Hodgkin referred to sodium and potassium structural channels which open and close under particular conditions. He pointed to the belief that phosphates provided the energy to pump ions across the membrane.²²⁸ Hodgkin's comments represent the midcentury understanding that neurophysiologists and biophysicists would collaborate with biochemists, anatomists and histologists to look for the mechanisms underlying nervous conduction. Together, using the tools, techniques, and language of the day, and not unlike du Bois-Reymond and Helmholtz a century before them, twentieth-century interdisciplinary teams of scientists would follow the reductionist imperative to describe nervous functionality as a relationship between physicochemical forms of energy.

²²⁶ Hodgkin, A. L., and A. F. Huxley. "A Quantitative Description of Membrane Current and its Application to Conduction and Excitation in Nerve." *The Journal of Physiology*, 117(1952):500-544, p. 502.

²²⁷ Hodgkin, A. L., Huxley, A. F., and B. Katz. "Measurement of Current-Voltage Relations in the Membrane of the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):424-448, pp. 426-427.

²²⁸ Hodgkin, A. L. "The Croonian Lecture - Ionic Movements and Electrical Activity in Giant Nerve Fibres." *Proceedings of the Royal Society of London B*, 148;930(1958):1-37.

Conclusion

Sherrington invoked evolutionary theory to explain purposiveness of reflex action as inborn adaptation to the environment.²²⁹ To Sherrington and his contemporaries, "purpose" became increasingly synonymous with "adaptation" of reflex reactions; in early twentiethcentury physiology, "purpose" no longer held the connotations of, as Sherrington would put it, "an informing spirit resident in the organism."²³⁰ Through their research and taken-for-granted endorsement of the electroconductive model of nervous functionality by Sherrington, Adrian, Hodgkin, Huxley and the many other neurophysiologists discussed in this chapter, a conceptual and philosophical shift occurred; with the aid of more sophisticated technology and the conception of the integrative synapse, the informing spirit was finally eradicated and ultimately replaced with the reductive materialism that du Bois-Reymond and Helmholtz vehemently advocated for the century prior. Lucas, Adrian, the Lapicques, Wedensky and Pavlov's attention to the temporal relations of nervous conductivity underwrote the basis for thinking about adaptive change in material terms, along with Sherrington's reframing of reflex arc activity as synaptic integration; Hill, Katz, Hodgkin, and Huxley's inquiries into the relationship between electric excitation and neuronal membrane potential further solidified the notion of nervous functionality as a set of physicochemical reactions. Incrementally, twentieth-century neurophysiologists removed God from the brain and co-created an electroconductive model for nervous functionality that built upon the neurophysiological project begun in the nineteenth century.

²²⁹ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, pp. 235-240; Swazey, Judith P. "Sherrington's Concept of Integrative Action." *Journal of the History of Biology*, 1;1(1968):57-89.

²³⁰ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, p. 236.

Sherrington's concept of reflex integration provided a theoretical framework for physiological functional adaptation by the nervous system. It included the idea of the nervous system as dynamically active, but organized and ordered, so necessarily well-coordinated. To be coordinated, something needed to be in control; that something was the cortex. Sherrington's integrative theory, however, considered adaptive change as occurring along unchanging predefined reflex paths. The Canadian neuropsychologist Donald Hebb (1904-1985) challenged that conception in *The Organization of Behavior* (1949) by suggesting additional components to neurophysiological adaptability. The Sherringtonian synaptic and electroconductive models of behavior allowed for Hebb to reframe the notion of functional adaptability along defined reflex paths into a model of functionality as incessantly plastic because of the nervous system's incessant process of learning and remembering, mediated through synaptic connectivity.

Although Sherrington mentioned "vital spirits" (referencing Descartes) once in *Integrative Action*, he modified the concept of vital forces by articulating a possible chemical "nutrient" necessary to maintain and provide energy for cellular life. Engaging with nineteenth-century energy discourses that was brought to bear on organic life through Helmholtz and others, Sherrington favored the idea of the active nervous system, espousing that chemical energy or a metabolic process of some form fuels activity in the brain. "The living cell," said Sherrington, "is constantly liberating energy in its function, and rebuilding its complex structure from nutrient material. Its life therefore an equilibrium of balanced katabolism and anabolism."²³¹ Sherrington's conceptualization of nervous system functionality was about more than maintaining a balanced equilibrium, however. He embraced a sense of progress and change in

 ²³¹ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906,
 p. 195; McIlwain, Henry. "Neurochemistry and Sherrington's Enchanted Loom." *Journal of the Royal Society of Medicine*, 77(1984):417-425.

which the balance point was constantly shifting and improving through the process of adaptation and interaction with the environment; he considered the nervous system "in a certain sense the highest expression of what the French physiologists term the *milieu interne*."²³²

Sherrington's systematic work on spinal reflex physiology as a way to understand nervous system functionality and the concepts and methods that emerged "allowed the problems of transmission to be brought to more definite terms. And so in the end reflex physiology and the electrophysiology of transmission merged when so long they had gone their independent ways."²³³ Sherrington's blend of anatomical and physiological investigation for understanding the coordination and control of nervous activity from receptor organ to conductive pathway to effector organ, however, would be sidelined for a predominantly electrophysiological approach as subsequent workers, using the new tools available to them, concerned themselves primarily with describing and constructing material explanations for how electricity propagated through nerve.

Du Bois-Reymond observed the impulse as change in electromotive force and described it as an altered state in the nerve. He speculated on the mechanism to account for the change in electromotive force and Helmholtz reframed the question in thermodynamic terms. Early and mid-twentieth-century neurophysiologists concerned with figuring out the mechanism of nervous conduction, how the impulse regenerates along an axon, how electrical potential differences are manifested, and with equating electrical potential differences with activity, engaged in the conservation of energy discussion started the century prior, albeit with new tools and language. They focused on making biophysical interpretations of neuronal function and moved away from

²³² Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, p. 4.
²³³ Denny-Brown, D. "The Sherrington School of Physiology." *Journal of Neurophysiology*, 20(1957):543-548, p.

²³³ Denny-Brown, D. "The Sherrington School of Physiology." *Journal of Neurophysiology*, 20(1957):543-548, p. 547.

comprehensive attempts to physiologically describe the function of the entire nervous system because of a reductionist, mechanistic imperative for deeper functional understanding at the cellular level, but also because they acknowledged the lack of knowledge to create unified theory of nervous system functioning.

Remarks by Katz reveal his belief in defining the nervous system in terms of coordination and control, yet concede his recognition that the field of neurophysiology had not yet reached the point of assembling a comprehensive theory of functional organization and thus must content itself with a reductive project based on a model of electrical conductivity. In a series of six public lectures titled "Transmission of excitation in nerve and muscle" delivered at University College London in 1947, Katz focused his remarks on "the question of which are the important physical and chemical properties of these tissues [nerves and nerve endings], upon what properties does their normal function depend, and what changes occur during the transmission of messages." He admitted to the general "lack of knowledge" of the "organisation of the central switchwork" performed by the central nervous system, which was "[t]he more elaborate part" compared to the peripheral nervous system in which he worked. The central nervous system, which he called the "central switching system" had the job of "sifting and sorting" the incoming signals "and deciding upon a proper response."²³⁴

Twentieth-century scientists increasingly turned towards physical principles to explain biological phenomena. Similar to how the "structural" and "informational" schools of the emerging field of molecular biology were dominated by physicists and chemists interested in biology, the leaders of the field of nervous conduction were primarily physicists who entered the

²³⁴ Typescript of "Lecture I - Transmission of Excitation in Nerve and Muscle," October 21, 1947, B.46, Bernard Katz papers, University College London, London, England, p.1.

biological realm through biophysics.²³⁵ The field of molecular biology originated, however, because of a pushback against the scientific order of strict reductionism inherited from physics and a social desire for scientific unity between physics and biology in the interwar years. The history of molecular biology concerns the formation of questions about the basis of biological life which combine biology with mathematics, physics, and chemistry.²³⁶

As the 1930s "Biotheoretical Gathering" symbolized marginalized scientists' desire to transcend the oppressive disciplinary boundaries between physics and biology, so too did some nervous system researchers at midcentury call for enhanced comingling of the physiological and anatomical study of the nervous system which was represented in Sherrington's *Integrative Action* but had subsequently fallen out of favor.²³⁷ For example, in his 1946 inaugural lecture as professor of anatomy at University College London, the English zoologist J. Z. Young (1907-1997), who a decade earlier had introduced Hodgkin, Huxley, Curtis and Cole to the squid giant axon, called for an end to the separation between anatomy from biochemistry and biophysics in the study of the nervous system.²³⁸ Young admitted that the framework of mechanism deriving from logic and later, physics "has been responsible for almost the whole of the triumph of mechanical science" but "[s]ome signs of strain in its use have for long been evidence in Physics, and it has often been held to be inadequate for Biology."²³⁹ Young wanted a modification to the mechanistic study of the nervous system; he said: "In order to describe our nervous system

 ²³⁵ For a detailed analysis and description of the birth and development of molecular biology, see Olby, Robert. *The Path to the Double Helix: The Discovery of DNA*. Seattle: University of Washington Press, 1974.
 ²³⁶ Abir-Am, Pnina Geraldine. "The Biotheoretical Gathering, Trans-Disciplinary Authority and the Incipient

Legitimation of Molecular Biology in the 1930s." *History of Science*, 25;1(1987):1-70.

²³⁷ Abir-Am, Pnina Geraldine. "The Biotheoretical Gathering, Trans-Disciplinary Authority and the Incipient Legitimation of Molecular Biology in the 1930s." *History of Science*, 25;1(1987):1-70.

²³⁸ Typescript of "Inaugural Lecture - Patterns of Substance and Activity in the Nervous System." J. Z. Young papers, 1946, 22/34 C.2.3 JZY ref A.3, University College London, London, England, p. 5; "The New Anatomy." *Nature*, 158;4205(1946):907.

²³⁹ Typescript of "Inaugural Lecture - Patterns of Substance and Activity in the Nervous System." J. Z. Young papers, 1946, 22/34 C.2.3 JZY ref A.3, University College London, London, England, p. 3.

plausibly, we must make further analysis of the pattern in which the substances are arranged within it, that is to say, study what is conventionally referred to as its anatomic, macroscopic and microscopic."²⁴⁰ Comparative biology, embryology and study of nerve degeneration and regeneration are critical allies, Young said, but it is important to remember that the substances of living material are "continually changing, taking part in activities" which are not necessarily related to their outside environment, but "directed towards the conservation of the pattern."²⁴¹

Hebb's work and the work of computational neural modelers shaped by cybernetic and information theories, made possible by widespread acceptance of the electroconductive framework, mark a midcentury turn toward privileging nervous activity patterns as the key to understanding behavior. The work of Sherrington, Adrian and the generation of neurophysiologists succeeding them seemed to fulfill a promise that the workings of body and mind could be explained in completely material terms, as a set of electrochemical reactions. As a result, many neuropsychologists and neurophysiologists readily accepted the disappearance of the self in the American psychologist B. F. Skinner's (1904-1990) black box located between stimulus input and behavioral output. Hebb's theory represents not only a paradigm shift, but a philosophical and metaphysical shift at midcentury. Shaped by Hegelian influence, Hebb helped reframe the notion of the self by assuming the actual functionality of the nervous system could be aligned with older conceptions of the mind; his theory was much more integrated with the philosophy of mind than the research described in this chapter.

 ²⁴⁰ Typescript of "Inaugural Lecture - Patterns of Substance and Activity in the Nervous System." J. Z. Young papers, 1946, 22/34 C.2.3 JZY ref A.3, University College London, London, England, p. 4.
 ²⁴¹ Typescript of "Inaugural Lecture - Patterns of Substance and Activity in the Nervous System." J. Z. Young

papers, 1946, 22/34 C.2.3 JZY ref A.3, University College London, London, England, p. 23.

Chapter 4

Hebb's union of psychology and neurophysiology

In 1949, the Canadian psychologist Donald Hebb (1904-1985) published *The Organization of Behavior*, his theory of neural activity change as the neuropsychological basis of learning and ideation which ultimately equated the physiology of behavior with the physiology of thought. His contributions, particularly the concept of the cell assembly, had a lasting legacy. In his 1894 Croonian lecture, the future Nobel Prize-winning Spanish neuroanatomist Santiago Ramón y Cajal presented a "connectionist view of neural organization," suggesting that circuits of cells work together in the brain's processing pathways. In the same lecture he postulated that the mechanisms of learning and memory had to do with enhanced synaptic connections between neurons.²⁴² The question of what was happening at the synapse occupied neurophysiologists and psychologists since then, and physiologically-informed theories of learning have consistently cited synaptic changes as crucial to its underlying mechanism. The notion of the Hebbian synapse continues to inform contemporary neuroscientific ideas about the plastic relation between the brain and the mind and remains an important guiding principle for experimental

²⁴² Jones refers to Ramón y Cajal's "connectionist view of neural organization." Jones, Edward G. "Santiago Ramón y Cajal and the Croonian Lecture, March 1894." *TINS*, 17;5(1994):190-192. See also, Ramón y Cajal, Santiago.

[&]quot;The Croonian Lecture: La Fine Structure des Centres Nerveux." *Proceedings of the Royal Society of London*, 55(1894):444-468; Ramón y Cajal, Santiago. *Nuevo Concepto de la Histología de los Centros Nerviosos*. Barcelona: Henrich, 1893; Cannon, Dorothy F. *Explorer of the Human Brain: The Life of Santiago Ramón y Cajal (1852-1934)*. New York: Henry Shuman, 1949, which contains of memoir of Ramón y Cajal by Sherrington.

studies and theoretical models attempting to elucidate the neurobiological basis of learning, memory and cognition.²⁴³

Hebb's work, an attempt to reconcile psychological theory with physiological evidence, serves as lens to appreciate the role theorizing and taken-for-granted assumptions play in neuroscience research design and interpretation. The debate he entered about whether human and animal intelligence were innate capacities or environmentally-determined was part of a larger discussion about the role of nature vs. nurture in the formation and expression of the self. His work also engaged with longstanding reflections about the nature of the mind-body interaction. Hebb brought together the electroconductive and subsequent materialist neurophysiological models of brain functionality that emerged from the works of du Bois-Reymond, Helmholtz, Sherrington, Adrian, Hodgkin, and Huxley, and others with psychological models of the mind described in this chapter. Hebb's neuropsychological model of the mind challenged yet also integrated neurophysiological models, becoming a critical link between physiology and psychology that eventually prepared the ground for a complex neurophysiologically-informed understanding of learning and memory.

Donald Olding Hebb, born in Nova Scotia in 1904, first considered a career in psychology in 1927, after reading the works of the Austrian neurologist and founder of psychoanalysis, Sigmund Freud (1856-1939).²⁴⁴ In 1928, he enrolled part-time in graduate studies at McGill while serving as a school principal in the suburbs of Montreal. In 1931, bedridden due to a tubercular infection in his hip, he studied Sherrington's *The Integrative*

²⁴³ See e.g., Nicoll, Roger A. "A Brief History of Long-Term Potentiation." *Neuron*, 93(2017):281-290; Sejnowski, Terrence J. *The Deep Learning Revolution*. Cambridge, MA: The MIT Press, 2018, pp. 101-102.

²⁴⁴ Donald Hebb to Walter J. Coville, July 2, 1963, 0000-2364.01.4.2, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada; Brown, Richard E., and Peter M. Milner. "The Legacy of Donald O. Hebb: More than the Hebb Synapse." *Nature Reviews Neuroscience*, 4(2003):1013-1019; Milner, Peter M. "The Mind and Donald O. Hebb." *Scientific American*, 268;1(1993):124-129.

Action of the Nervous System and Pavlov's *Conditioned Reflexes*, which had been translated to English in 1927. In 1932, Hebb produced an M.A. thesis describing spinal reflexes as the result of Pavlovian conditioning. He became disenchanted with Pavlovian techniques, however, after spending time conditioning dogs in the physiological laboratory of Russian émigré Leonid Andreyev (1891-1941), who came to McGill after working in Pavlov's laboratory.²⁴⁵ Hebb began his Ph.D. with the eminent American neuropsychologist Karl Lashley (1890-1958) at the University of Chicago in 1932, completing it in 1936 at Harvard, where Lashley had moved. He spent the next two years working with patients of the American-Canadian neurosurgeon Wilder Penfield (1891-1976) at the Montreal Neurological Institute. He also spent five years at the Yerkes Primate Center in Florida, assessing emotional responses in chimpanzees. While in Florida, Hebb began writing *The Organization of Behavior*; he completed it in 1948 while head of the department of Psychology at McGill University.²⁴⁶

As the historian Roger Smith noted, the history of psychology reveals debates about the proper way to understand the mind and human self-knowledge.²⁴⁷ According to Hebb, the psychology of American psychologists Edward Thorndike (1874-1949), John Watson (1878-1958), and Clark Hull (1884-1952) attempted "somehow to make all thought a relatively simple matter of learning, to make it *intelligible* by the mechanisms of association."²⁴⁸ Hebb, by engaging with the behaviorist conception of association, reified his predecessors' framing of human cognition as fundamentally a process of learning. Using neurophysiological evidence to create and support his theory of the neural organization of behavior as represented through

²⁴⁵ Brown, Richard E., and Peter M. Milner. "The Legacy of Donald O. Hebb: More than the Hebb Synapse." *Nature Reviews Neuroscience*, 4(2003):1013-1019; Milner, Peter M. "The Mind and Donald O. Hebb." *Scientific American*, 268;1(1993):124-129.

²⁴⁶ Brown, Richard E. "The Life and Work of Donald Olding Hebb: Canada's Greatest Psychologist." *Proceedings of the Nova Scotian Institute of Science*, 44;1(2007):1-25.

²⁴⁷ Smith, Roger. Between Mind and Nature: A History of Psychology. London: Reaktion Books, 2013, p. 13.

²⁴⁸ Hebb, D. O. "On Human Thought." Canadian Journal of Psychology, 7;3(1953):99-110, p. 101.

activity patterns (re)inscribed through a synaptic learning mechanism, Hebb helped solidify the contemporary neuroscientific notion that human and animal capacity—and incessant endeavor—to learn and remember lies at the very essence of who we are. With evidentiary support from the electroconductive model firmly established by Sherrington and his colleagues, Hebb helped reconfigure the self as in a constant process of neurophysiological becoming.

The Organization of Behavior formulated the generalized process of perception as patterns of activity in the phase sequence and accounted for the localization of experience in the cell assembly memory trace. Hebb addressed the gripes of his teacher Lashley and the Gestaltists about the static reflex notion of learning and included a role for dynamic patternmaking shaped by experience and autonomous central processes. He followed from Sherrington in framing the mind-body problem as one of integration, but departed from the Sherringtonian and behaviorist reliance on mechanism and atomism to explain cognition, embracing instead a field theory of wholes underwritten by electrical nervous activity which linked psychological ideation with material explanatory power. Hebb's neuropsychological theory of behavior as encompassing both mental and neural activity centers the nervous system's capacity for learning and remembering as essential to the nature of the relationship between brain and mind. Considering how to understand the mind leading up to behaviorism

The idea that memories have both spatial and temporal dimensions can be traced back to the philosophy of Aristotle (385-323 BC), who said that conservation and retrieval were the two distinct stages of memory. Since Aristotle believed only humans were conscious of time, and that recollecting requires awareness and logical thought, he said that only humans have memories, whereas animals have mental pictures. Aristotle's disassociating of experience and the elements required to render it to memory contributed to nineteenth-century explanations of deja vu and

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confabulation, the practice of making up stories to fill in memory gaps. The theologian St. Augustine (354-430), a Platonic idealist who influenced Descartes and Freud, wrote that the purpose of memory is to preserve and revive experience. Descartes said that recollection was due to "facilitation" and that recognition requires active participation of the mind; here arose the notion of consciousness. In *Human Nature*, the English philosopher Thomas Hobbes (1588-1679) wrote that forgetting is like walking away from something and it gradually losing detail; memory is related to imagination, he said, except that in memories we suppose a time that has passed. The English philosopher John Locke (1632-1704), inspired by Aristotelian associationism and eighteenth-century English physiologists like David Hartley (1705-1757), thought that emotions could anchor ideas together in the mind.²⁴⁹

Particularly after the 1820s, studies focused on the content of memory and its laws of retention and association. Clinical observations paralleled the psychological debate around memory, placing confabulation, deja vu and memory delusions under the categories of "amnesia" and "paramnesia." These prototypical cases were very important to theoretical models. In France, an active model of the mind derived from the philosophies of Pierre Laromiguière (1756-1837) and Pierre-Paul Royer-Collard (1763-1845) who believed that memories had to be taken up in consciousness—we can only remember that which is taken up in our mind. The French psychologist Théodule-Armand Ribot (1839-1916) would combine these ideas with English associationism at the end of the century.²⁵⁰ The French memory studies were predominantly studies of forgetting, due in part to a French cultural fascination with forgetting

 ²⁴⁹ Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996.

²⁵⁰ Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996.

and nostalgia.²⁵¹ Ribot's 1882 work, *Diseases of Memory: An Essay in the Positive Psychology*, dealt mostly with forgetting, but included a section on hypermnesia—too much memory—which he thought of as pathological. Ribot, in including a moral dimension to his work, attempted to define the amount of memory that was just right. A positive psychologist who subscribed to the doctrine of cerebral localization in an attempt to anchor his work in the more established discipline of neurobiology, Ribot's work was part of the nineteenth-century French discourse about conserving and reproducing the past, a discourse that intertwined with what it meant to be normal in the present.²⁵² Ribot advised the French psychologist Alfred Binet (1857-1911), who would later go on to devise tests for the measurement of intelligence, early in Binet's career.²⁵³

Associationism dominated British views on memory until the end of the nineteenth century. The philosopher John Fearn (1758-1837) asserted that attention was needed to lay down memories while the philosopher James Mill (1773-1836) wrote that memories contain ideas that are connected through associations. In the middle of the century, the philosopher Alexander Bain (1818-1903) attempted to adapt Locke's associationism into an objective experimental psychophysiology following epistemological debates between the German anatomist and physiologist Franz Joseph Gall (1758-1828) and French physiologist Jean-Pierre-Marie Flourens (1794-1867) about cerebral localization theory and the material basis of the mind. Adding a physiological component to associationism, Bain believed that each idea, habit, or recollection had a corresponding physical basis in the body. Bain studied the associations between motor and

²⁵² Roth, Michael, S. "Remembering Forgetting: Maladies de la Memoire in Nineteenth-Century France."
 Representations, Special Issue: Memory and Counter-Memory, (1989):49-68; See also, Ribot, T. H. *Diseases of Memory: An Essay in the Positive Psychology*. London: Kegan Paul, Trench & Co, 1882.
 ²⁵³ Smith Poger, "Shaping Brychology," In *Retween Mind and Natures: A History of Brychology*, 70, 101, London.

²⁵¹ Roth, Michael, S. "Remembering Forgetting: Maladies de la Memoire in Nineteenth-Century France." *Representations, Special Issue: Memory and Counter-Memory*, (1989):49-68.

²⁵³ Smith, Roger. "Shaping Psychology." In *Between Mind and Nature: A History of Psychology*, 70-101. London: Reaktion Books, 2013.

sensory activity and, as early as 1872 postulated that growth at the junctions between nerve cells could account for memory.²⁵⁴

Bain, an intellectual follower of the English philosopher John Stuart Mill (1806-1873), who understood the way we talked about the human mind had profound social and political consequences, privileged activity over sensation; for Bain, experience is an active affair, and he maintained that learning can occur by adjustment through trial and error. Beginning at the turn of the century, American psychologists Edward Thorndike and (later) B. F. Skinner (1904-1990) tested the idea that behavior informs learning through the studies of operant conditioning, a method to induce learning in rats through reinforcement and punishment.

Bain's mechanistic model was reinterpreted in evolutionary terms after midcentury by the British philosophers Herbert Spencer, G. H. Lewes (1817-1878), and neurologist John Hughlings Jackson. Spencer, also shaped by John Stuart Mill's utilitarianism which reduced scientific laws to psychological notions of associationism, attempted to create a unifying theory of evolution by bridging the principles of biology, psychology, sociology and ethics through his synthetic philosophy. Spencer believed he solved the debate between idealists and empiricists by claiming that individual minds make knowledge using predetermined categories, but that these categories are actually made by reasoning from previous observations or experiences through an evolutionary process.²⁵⁵ Spencer argued that complex integrated systems arise through the process of evolution; organization can be thought of as adaptation produced over time through natural laws. Accordingly, his project from the end of the nineteenth century was an attempt to

²⁵⁴ Finger, S. "Santiago Ramón y Cajal: From Nerve Nets to Neuron Doctrine." In *Minds Behind the Brain: A History of the Pioneers and Their Discoveries*, 198-216. Oxford: Oxford University Press, 2004. See also, Bain, Alexander. *Mind and Body: The Theories of Their Relation*. London: Henry S. King, 1872; Young, Robert Maxwell. *Mind, Brain and Adaptation in the Nineteenth Century*. New York: Oxford University Press, 1970.

²⁵⁵ In the 1890s, the German philosopher and mathematician Gottlob Frege reacted against this kind of philosophical reasoning, beginning the movement of analytic philosophy which developed and maintained a strong foothold in the twentieth century.

explain how parts serve wholes through an exploration of individual and social life. Therefore, a study of the mind, said Spencer, must show its evolution and adaptation through interaction and experience.²⁵⁶

In his influential 1890 monograph *The Principles of Psychology*, the American pragmatist and functional psychologist William James (1842-1910) stated that "few recent formulas have done more real service of a rough sort in psychology" than the Spencerian notion of "the adjustment of inner to outer relations."²⁵⁷ Both Pavlov and Lashley, despite their differing opinions on the role of the reflex in the organization of the central nervous system, acknowledged Spencer as suggesting that instincts can be explained by the reflex mechanism.²⁵⁸

The reflex concept helped neurophysiologists and psychologists explain automatic behaviors and many accepted the reflex concept as helpful in understanding "higher order" mental processes. In the 1820s, the French physiologist François Magendie (1783-1855) and his British rival Charles Bell showed contemporaneously the differentiation between sensory nerves and motor nerves to and from the spinal cord. The Bell-Magendie law stated that electrical impulses carried by these nerves travel in only one direction—toward the spinal cord in the case of sensory nerves, and the reverse for motor nerves.²⁵⁹ The 1830s debates between English physiologist Marshall Hall (1790-1857) and German physiologist Johannes Müller (1801-1858)

²⁵⁶ Smith, Roger. "The Mind's Place in Nature." In *Between Mind and Nature: A History of Psychology*, 39-69. London: Reaktion Books, 2013.

 ²⁵⁷ James, William. *The Principles of Psychology*, Vol. 1. New York: Henry Holt and Company, 1890, p. 6.
 ²⁵⁸ Pavlov, I. P. *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex*. Edited and translated by G. V. Anrep. Oxford: Oxford University Press, 1927, p. 9; Lashley, K. S. *Brain Mechanisms and Intelligence: A Quantitative Study of Injuries to the Brain*. Chicago: The University of Chicago Press, 1929, p. 163.

²⁵⁹ Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906, p. 38.

resulted in widespread understanding of the reflex as the elementary unit of nervous function, which helped to provide a material explanation of purposive movement.²⁶⁰

John Hughlings Jackson expanded on Bain's experimental work, invoking evolutionary neurophysiological ideas from Spencer when examining hemispheric-injury and epilepsy in his patients. Like the French physician and anatomist Paul Broca (1824-1880) and French neurologist Jean-Martin Charcot (1825-1893), Jackson believed in cortical localization, investigating the motor and language centers of the brain while attempting to bridge organic and functional theories of disease through his emphasis in the rigorous scientific study of the nervous system.²⁶¹ In the 1870s, experiments with cortical electrical stimulation by Germans Eduard Hitzig (1838-1907), a neurologist, and Gustav Theodor Fritsch (1838-1927), an anatomist, as well as by the British neurologist David Ferrier, proved cerebral localization of function but by that decade, Jackson became disillusioned with the idea that the reflex arc could explain more complex functions like language.²⁶²

Meanwhile, in Germany a rebellion against the idealist philosophy of Hegel drove some scholars interested in sensation and mental processes to turn to the successful methods of physiology for inspiration. In the final two decades of the nineteenth century, the German physiologist Wilhelm Wundt (1832-1920), who studied under Emil du Bois-Reymond and was later assistant to Hermann von Helmholtz, created an experimental program which focused on

²⁶¹ Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996; York, George K. and David A. Steinberg. "Hughlings Jackson's Neurological Ideas." *Brain*, 134(2011):3106-3113. See also, Jackson, John Hughlings. *Selected Writings of John Hughlings Jackson*, Vol. 1. Edited by J. Taylor. London: Hodder & Stoughton, 1931.
²⁶² Smith, Roger. "The Mind's Place in Nature." In *Between Mind and Nature: A History of Psychology*, 39-69. London: Reaktion Books, 2013.

²⁶⁰ Fearing, Franklin. "Marshall Hall." In *Reflex Action: A Study in the History of Physiological Psychology*, 122-145. Cambridge, MA: The MIT Press, 1970; Smith, Roger. *Inhibition: History and Meaning in the Sciences of Mind and Brain*. Berkeley: University of California Press, 1992, pp. 38, 68.

the psychological aspects of sensation as a source of knowledge independent from physiology. Helmholtz's work in the experimental physiology of sensation, including his speed of nervous conduction studies, showed Wundt that measuring time can be a proxy for understanding the activity of mental processes.²⁶³

In his Leipzig laboratory, Wundt tried to create both (1) a unified philosophy using the methods of the natural sciences to attack psychological questions, and (2) a program of experimental psychology using the techniques and instruments of reaction time studies and methods of psychophysics developed by his predecessors. Considering the mental act as a fact of reality produced through evolutionary and social processes, Wundt wanted to establish psychology as an independent discipline separate from physiology, which could ask philosophical questions through experimentation. For example, he devised experiments which instructed human participants (usually his students) to turn a key in an electrical circuit when they perceived a difference in brightness of light.²⁶⁴

In the U.S., distinct schools of psychology incorporated experimentation from Germany, clinical evidence from France, and the evolutionary perspective from Britain as part of a general project promoting the betterment of society and ideals of democracy through education and intelligence testing. Building off experimental work studying the effect of attention on "muscular" and "sensorial" reaction time in humans, the English psychologist E. B. Titchener (1867-1927) and his structuralist school of psychology in the U.S. contended that the longer "sensorial" reaction time amounted to a mental phenomenon, distinct from biological motor

²⁶³ Smith, Roger. "Shaping Psychology." In *Between Mind and Nature: A History of Psychology*, 70-101. London: Reaktion Books, 2013; Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience*. Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010, pp. 100-101.

²⁶⁴ Smith, Roger. "Shaping Psychology." In *Between Mind and Nature: A History of Psychology*, 70-101. London: Reaktion Books, 2013; Mandler, George. "The Birth of Modern Psychology: Wilhelm Wundt and William James." In *A History of Modern Experimental Psychology: From James and Wundt to Cognitive Science*, 51-75. Cambridge, MA: The MIT Press, 2007.

movement, though both are subject to evolutionary processes. Titchener trained in Leipzig, established by Wundt as the capital of experimental psychology. Breaking from Wundt's philosophy, however, Titchener's brand of structural psychology held that experiments can reveal the elementary constituents of the psychic mind.²⁶⁵

The structuralists considered themselves morphologists of the mind, using introspection in an attempt to understand the structural elements—of sensations, ideas, and feelings, for example—of the mind. In 1885, the German psychologist Hermann Ebbinghaus (1850-1909) tried to study memory experimentally and quantitatively by examining recall of nonsense syllables. Consistent with turn-of-the-century enthusiasm for psychometric and statistical testing and quantitative analysis, Ebbinghaus and others studying memory assumed that quantification was the best way towards understanding memory disorders in individuals.²⁶⁶ Titchener contended that structural psychology aligned well with the work of experimental psychologists like Ebbinghaus, whereas the school of functional psychology was doomed unless it could be paired with experimentation.²⁶⁷

Whereas structural psychology maintained that there are typical experiences which can be reduced to irreducible elements that can be classified with the help of experimentation, functional psychology, on the other hand, took the psycho-physical organism as its basal element. Functional psychology was concerned with the relations of the functioning psycho-

²⁶⁵ Smith, Roger. "Shaping Psychology." In *Between Mind and Nature: A History of Psychology*, 70-101. London: Reaktion Books, 2013; Boring, Edwin G. "The Beginning and Growth of Measurement in Psychology." *Isis*, 52;2(1961):238-257. See also, Smith, Roger. *The Fontana History of the Human Sciences*. London: Fontana Press, 1997.

²⁶⁶ Berrios, German E., and John Hodges. *Memory Disorders in Psychiatric Practice*. Cambridge: Cambridge University Press, 2000, pp. 10-12.

²⁶⁷ Titchener, E. B. "Simple Reactions." *Mind*, 4(1895):74-81; Titchener, E. B. "The Postulates of Structural Psychology." *Philosophical Review*, 7(1898):449-465; Titchener, E. B. "On 'Psychology as the Behaviorist Views It." *Proceedings of the American Philosophical Society*, 53(1914):1-17; Calkins, Mary Whiton. "A Reconciliation Between Structural and Functional Psychology." *Psychological Review*, 13(1906):61-81.

physical self with its environment. Deriving from pragmatism and its focus on process and progress, functionalism assumed function, or human action, as having an end, a purpose.²⁶⁸

In the last decade of the nineteenth century the American philosopher, functionalist and pragmatist John Dewey (1859-1952) arrived at the University of Chicago, an institute set up with funds from the American business magnate John D. Rockefeller (1839-1937) to address the city's social ills through education and psychological expertise. Dewey, committed to a functional explanation for adaptation, reframed the reflex concept as a process and a means to an end which helps us understand the whole organism as acting to adapt to its environment. Shaped by his Hegelian and evolutionary outlook, Dewey understood the mind as historically unfolding through a process of adaptive transformation. Dewey sympathized with other functionalists like James and the American sociologist Albion Small (1854-1926) who saw society as a stable system, in which everything has a purpose in helping it function. Dewey, Small and James helped transform education, sociology and philosophy in the U.S.²⁶⁹

Functionalists like James sought to explain the mind as a product of an evolutionary process. Opposed to biological determinism and responding to late nineteenth-century concerns over the social ills of industrialization, urbanization and immigration, James used Spencerian and Darwinian-inspired notions of adaptation to consider non-mechanistic, non-reductionist ways for individuals to adapt to rapid social change. For James, consciousness is experienced in relation to the environment.

²⁶⁸ Calkins, Mary Whiton. "A Reconciliation Between Structural and Functional Psychology." *Psychological Review*, 13(1906):81-81. See also, Boring, Edwin G. *A History of Experimental Psychology*. New York: D. Appleton-Century Company, 1929.

²⁶⁹ Smith, Roger. *Between Mind and Nature: A History of Psychology*. London: Reaktion Books, 2013, pp. 66-67, 97-98.

As an originator of the U.S. philosophical tradition of pragmatism arising in the 1870s, James believed in the power of human action for directing nature and the cosmos toward the wellbeing of humanity. He rejected the notion that conscious thought could accurately describe or mirror reality, instead emphasizing the practical, functional uses to which ideas could be assembled to solve problems. Thus, he helped conceptualize the idea that by measuring individual differences and how individuals adapt to their environment one could develop a conscious system of "minded behavior" which would help individuals learn, remember and adjust to a rapidly-changing society.²⁷⁰

James launched his individualistic philosophy at the turn of the century, hoping to replace religious life with an investigation of psychic life. For James this meant an embrace of anarchy "in the good sense" in order to reform the world; to him, "ideals were particular and personal rather than universal or absolute, and they were historically contingent."²⁷¹ Acknowledging no absolute truths, James' pragmatism expected individuals to weigh truths and values, to create their own truths and ethical guidelines as time moved on and contexts changed. James' idea of a pluralistic pragmatism posited that individuals had to make sense of the world around them—an individual character must interact with a society in flux to construct their own realities. These new individuals, hoped James, would spark political action, helping "to rekindle the historically contingent ideals of pluralism and tolerance."²⁷²

James' pragmatic views reflected a broader modernist and Progressive Era emphasis on the idea of a "selection" of the self. Beginning in the nineteenth century and up through and

²⁷⁰ Coon, Deborah. "'One Moment in the World's Salvation.' Anarchism and the Radicalizing of William James." *The Journal of American History*, 83;1(1996):70-99; Musolf, Gil Richard. "William James and Symbolic Interactionists." *Sociological Focus*, 27;4(1994):303-314.

²⁷¹ Coon, Deborah. "One Moment in the World's Salvation' Anarchism and the Radicalizing of William James." *The Journal of American History*, 83;1(1996):70-99, p. 92.

²⁷² Coon, Deborah. "One Moment in the World's Salvation.' Anarchism and the Radicalizing of William James." *The Journal of American History*, 83;1(1996):70-99, p. 99.

immediately following World War II, Western ideological persuasions focused on using rationalist knowledge to control the individual and the structure of society and to influence the process of individual and sociological self-construction. From its beginnings as a discipline, psychology was concerned with *doing*, not just epistemology. During World War I, psychologists contributed to the war effort by assisting with personnel selection. In the interwar years, social psychologists, adopting a behaviorist bent, applied statistical methodology to develop a concept of normalizing by engaging with massive datasets and, through their selfconscious desire to achieve an air of scientific objectivity akin to the natural sciences, reified the notion of intelligence through recourse to quantification. Some psychologists, like James, believed in the malleability of the self. So too did Sigmund Freud, who created psychoanalytic theory by transforming the biological theory of instincts in a rationalist theory of psychic evolution from innate biological, instinctual life. Others, like the English statisticians and eugenicists Francis Galton (1822-1897), Karl Pearson (1857-1936), and Charles Spearman (1863-1945), shaped also by Darwin's evolutionary biology, insisted on the heredity of intelligence, defining it as stable throughout one's life and focusing on how to craft social policy around individual capacities and differences.²⁷³

Intelligence quotient (IQ) testing, the first technologizing of the Darwinian imperative to carry human evolution forward, emerged from Spearman's technical expansion of Galton's fears of the degeneration of British society as well as from Alfred Binet and French psychologist Théodore Simon's (1872-1961) contributions to the science of education in France at the turn of

²⁷³ Smith, Roger. "Psychological Society." In *Between Mind and Nature: A History of Psychology*, 102-136. London: Reaktion Books, 2013; Smith, Roger. "The Individual and the Social." In *The Fontana History of the Human Sciences*, 746-804. London: Fontana Press, 1997. See also, Sulloway, Frank J. *Freud, Biologist of the Mind: Beyond the Psychoanalytic Legend*. Cambridge, MA: Harvard University Press, 1992.

the century.²⁷⁴ The eugenics movement in Britain developed at a time of rapidly changing ideologies which paralleled rapidly changing social and political circumstances; eugenicists tied their beliefs about heredity and society to their dissatisfaction with the ruling class' complete political power. The coincident prominence of social Darwinism, which also scapegoated the lower classes as moral degenerates and drains to the economy, helped provide the conditions for eugenics' influence.²⁷⁵

Through the eugenics debate about intelligence, Galton pit "nature" and "nurture" against each other. He believed in the stronger influence of nature and tried to use his research to promote this idea. He said that heredity, not environment, determined individual differences. Galton's belief in nature over nurture was also in opposition to the Victorian self-help movement, reflected in the work of Scottish reformer Samuel Smiles (1812-1904). The ethos of self-help, placing onus on the individual to cultivate moral character and conduct, also supported the belief that environment had an important influence on childhood development. Smiles, therefore, placed great value on the importance of education to influence good habits of mind, suggesting a plasticity of the self.²⁷⁶

Pearson's bell curve was part of the Galtonian project to show social ills were due to individual differences and failings, not to the structure of social arrangements. Spearman, a psychologist who studied with Wundt, developed the concept of an innate and unitary "general intelligence" (g) and created psychometry to test it. Through Spearman and Binet's work, intelligence transformed into the cause of ability and came to denote a scientific notion of reason.

²⁷⁴ Smith, Roger. "Psychological Society." In *Between Mind and Nature: A History of Psychology*, 102-136. London: Reaktion Books, 2013.

²⁷⁵ MacKenzie, Donald. "Eugenics in Britain." Social Studies of Science, 6(1976):499-532.

²⁷⁶ Travers, T. H. E. "Samuel Smiles and the Origins of 'Self-Help': Reform and the New Enlightenment." *Albion: A Quarterly Journal Concerned with British Studies*, 9;2(1977):161-187.

The concept of intelligence also helped link humans to animals as different in degree, not in kind. The Canadian-Scots evolutionary biologist and physiologist George Romanes (1848-1894) wrote of intelligence as the capacity to adapt to changing circumstances. Only humans could possess reason, but both animals and humans had intelligence. This turn-of-the-century concept of intelligence opened the door for animal experimentation to make general claims about intelligence.²⁷⁷

In the early years of the twentieth century, successors of reaction time studies began to adapt their experiments to animal subjects. Bolstered by the evolutionary notion that humans have similar basic biological processes as animals, comparative psychologists became interested in the behavior of animals. The American John Watson led the charge in articulating the principles of the behaviorist school of psychology, claiming that a scientific psychology must avoid the epistemological solipsism of structural and functional psychology which explained mental processes in terms of states of consciousness. The behaviorists were not interested in the nature of consciousness; they maintained that only by examining the behavioral manifestations of internal mental processes can a rigorous, autonomous scientific psychology be truly useful. By emphasizing mental functions, behavioral psychology focused on how the mind gets expressed through what we *do*, how we behave. In his influential 1913 paper "Psychology as the behaviorist views it," Watson declared the goal of behaviorism was to predict and control behavior.²⁷⁸ Watson's behavioristic psychology sided with nurture over nature and was consistent with a conceptualization of the malleable self.

²⁷⁷ Smith, Roger. "Psychological Society." In *Between Mind and Nature: A History of Psychology*, 102-136. London: Reaktion Books, 2013.

²⁷⁸ Watson completed his graduate studies in the University of Chicago philosophy department headed by Dewey. After 1930, Watson's brand of behaviorism fell out of favor; it was replaced by the positivist neobehaviorism of Tolman, Hull and Skinner until about 1955-60, when behaviorism was eclipsed by the advent of humanistic psychology and the cognitive revolution. Smith, Roger. "Varieties of Science." In *Between Mind and Nature: A History of Psychology*, 137-170. London: Reaktion Books, 2013. See also, Watson, John B. "Psychology as the

The British philosopher and mathematician Bertrand Russell (1872-1970), in his 1921 *Analysis of the Mind*, agreed with Watson—and thanked him in the preface for his "many valuable suggestions" on the manuscript—in the denial of the real existence of images produced by the mind, but sided more with James and the "new realists" when articulating his main thesis that the mind is actually a collection of connections between sense-data, which have meaning through their particular relations. In other words, consciousness, according to Russell, is constructed from the complex interrelations of sensations and images, which have no meaning by themselves.²⁷⁹

Russell cited Sherrington's spinal transection (i.e., spinal severing) experiments with dogs as supporting the James-Lange theory that emotions *are* the feelings of bodily changes that occur during perception. In 1900, Sherrington severed the spinal cord of five dogs in the lower cervical region, cutting off the central nervous system from the thoracic, abdominal and pelvic viscera, while leaving certain cranial nerves (i.e., from the brain) intact. That these dogs demonstrated emotions signifying fear and rage suggested to Sherrington that the psychic part of emotion from the brain precedes the visceral reaction, not the other way around, as the James-Lange theory postulated. Russell sided with the American psychologist James Angell (1869-1949), however, in interpreting that Sherrington's observations did not disprove the James-Lange theory. Angell suggested that the dogs' display of emotion might have be due to past experience, a reflection of habits generated through previous stimulation of cerebral reflex arcs. Assuming Angell's interpretation a fair one, Russell stressed that an analysis of emotion must account for

Behaviorist Views It." *Psychological Review*, 20(1913):158-177; Watson, John B. *Behavior: An Introduction to Comparative Psychology*. New York: Henry Holt, 1914; Watson, John B. *Behaviorism*. New York: Norton, 1924; Watson, John B. *Psychology from the Standpoint of a Behaviorist*. Philadelphia: J. B. Lippincott, 1919; O'Donnell, John M. *The Origins of Behaviorism: American Psychology, 1870-1920*. New York: New York University Press, 1985.

²⁷⁹ Russell, Bertrand. *The Analysis of Mind*. London: George Allen & Unwin, 1921, pp. 6, 9-40. See also, Russell, Bertrand. *Philosophy*. New York: W. W. Norton & Company, 1927.

the dynamic processes underlying the occurrence of the emotion, the ingredients of which "are only sensations and images and bodily movements succeeding each other according to a certain pattern."²⁸⁰ For Russell, the causal dependence or independence of mind and matter bears little relevance, what is important, rather, is the meaning created through experience as we interact with the world.

B. F. Skinner claimed to be persuaded by the positivist stimulus-response (S-R) analysis of behaviorism as a result of Russell's accounts linking meaning to connections and relations between cause and effect.²⁸¹ Thorndike's work had established a model for the scientific assessment of learning in animals and was part of the broader shift toward replacing references to reason with intelligence, will with motivation, and mind with behavior. Thorndike, like Pavlov, demonstrated how to correlate changes in animal behavior with changes in physical stimuli as the foundation of a neural connectionist theory of learning, but unlike Pavlov, ignored autonomous central processes that might occur between afferent and efferent processes.²⁸² Thorndike hypothesized changes in synaptic resistance facilitating or hindering transmission of a neuron's electrical impulse as the possible mechanism accounting for his associative laws of

²⁸⁰ Russell, Bertrand. "Emotions and Will." In *The Analysis of Mind*, 279-286. London: George Allen & Unwin, 1921, p. 284. See also, Russell, Bertrand. *Philosophy*. New York: W. W. Norton & Company, 1927; Angell, James R. "A Reconsideration of James's Theory of Emotion in the Light of Recent Criticisms." *Psychological Review*, 23;4(1916):251-261; Sherrington, Charles S. "Experiments on the Value of Vascular and Visceral Factors for the Genesis of Emotion." *Proceedings of the Royal Society of London*, 66(1900):390-403.

²⁸¹ In a letter to Hebb, Skinner said his criticism of then-current physiological explanations of behavior emerged from positivism. He wrote, "Somewhere during the 1920s Bertrand Russell said something to this effect: 'The concept of the reflex has the same status in psychology as the concept of force in physics.' There, in a nutshell, is my thesis." The concept of force helped physicists find connections between sense-data, as the reflex concept had done for psychologists. B. F. Skinner to Donald Hebb, November 7, 1958, 0000-2364.01.44, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada; Moxley, Roy A. "Some Early Similarities and Later Differences Between Bertrand Russell and B. F. Skinner." *The Behavior Analyst*, 26(2003):111-130.
²⁸² Smith, Roger. "Varieties of Science." In *Between Mind and Nature: A History of Psychology*, 137-170. London: Reaktion Books, 2013.

acquired behavior and learning. The "law of effect" and "law of exercise," in other words, might be explained by the strengthening or weakening of neuronal connections.²⁸³

In the 1930s, the experiments of Skinner, along with those of fellow American neobehaviorist psychologists like Clark Hull, Edward Tolman (1866-1959), and Kenneth Spence (1907-1967) solidified the study of learning as the core of U.S. psychology research.²⁸⁴ Tolman introduced the concept of the nonphysiological "intervening variable" to account for purposive behavior and the animal's complex relationship with the environment which was lost by focusing solely on the stimulus and its response.²⁸⁵ Despite differences between the neobehaviorists, they shared a common focus of relating behavioral responses (of animals, including humans) to environmental happenings controlled by the experimenter, like rewards and punishments at particular temporal intervals. Skinner, Tolman and Hull correspondingly employed hypothetical intervening variables, motivational and attentional "drives", or causal laws to account for a learning mechanism which connects and associates—through reflex conditioning—stimulus with response as an organism interacts with its environment.²⁸⁶

Hebb sympathized with behaviorists' conception of learning, but recognized that a connectionist theory of learning did not adequately account for recent neurophysiological evidence nor the generalization of perception advocated for by Gestalt psychologists and his teacher Lashley. Hebb saw a role for both nature and nurture, innate structure and learning, and

²⁸³ Thorndike, Edward L. *Animal Intelligence: Experimental Studies*. New York: MacMillan, 1911, pp. 244-250. MacDougall presented an idea of reduced synaptic resistances in his drainage theory. McDougall, W. "The Nature of Inhibitory Processes Within the Nervous System." *Brain*, 26;2(1903):153-219.

²⁸⁴ Smith, Roger. "Varieties of Science." In *Between Mind and Nature: A History of Psychology*, 137-170. London: Reaktion Books, 2013. For the difference between Thorndike's theory of associative connections vs. Pavlov's theory of conditioned responses, see Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. 198.

²⁸⁵ Smith, Roger. "Varieties of Science." In *Between Mind and Nature: A History of Psychology*, 137-170. London: Reaktion Books, 2013.

²⁸⁶ Spence, Kenneth W. "Foreword to the Seventh Printing." In *Principles of Behavior: An Introduction to Behavior Theory*, by Clark L. Hull, vii-xvii. New York: Appleton-Century-Crofts, 1943.

The Organization of Behavior attempted to find a middle ground between the roles of heredity and environment in shaping a physiologically-grounded theory of behavior as changing patterns of neuronal activity.

Shifting from behaviorism and the stable route assumption

In 1934, Hebb moved to Chicago to conduct his doctoral studies with Lashley.²⁸⁷ Lashley, who worked for many years at the University of Chicago, never sympathized with the Progressive ideals of the American school of psychobiology centered there. Lashley was concerned with "pure" understanding, not social engineering nor aligning the discipline with the promotion of social progress. His public adherence to hereditarianism and insistence that the innate structure of the organism determines how it learns reflected his private political views, which included opposition to racial integration, social reform, and political change.²⁸⁸ Lashley also explicitly rejected psychological theorizing and irreducible concepts like mind and consciousness used by his psychobiologist colleagues. According to Lashley, a truly objective psychology must incorporate a physiological approach.²⁸⁹

While at the University of Chicago Hebb completed an unpublished manuscript titled "Scientific method in psychology: A theory of epistemology based on objective psychology," which, echoing Lashley, called for a physiologically-informed psychology. The manuscript rallied for an objective psychology based on human (and animal) activity to replace its traditional reliance on (or, in the case of behaviorism, objection to) theory of mind. To Hebb, attending to

 ²⁸⁷ Hebb moved with Lashley to Harvard in 1935; he received his Ph.D. from Harvard in 1936. Dewsbury, Donald
 A. "The Chicago Five: A Family Group of Integrative Psychobiologists." *History of Psychology*, 5;1(2002):16-37.
 ²⁸⁸ Weidman, Nadine M. "Psychobiology and Progressivism" and "Psychobiology and its Discontents: The Lashley-

Herrick Debate." In *Constructing Scientific Psychology: Karl Lashley's Mind-Brain Debates*, 86-118. Cambridge: Cambridge University Press, 1999.

²⁸⁹ Weidman, Nadine M. "Public Science and Private Life." In *Constructing Scientific Psychology: Karl Lashley's Mind-Brain Debates*, 160-175. Cambridge: Cambridge University Press, 1999.

activity would help reconcile psychology with physiology and was the only way forward for understanding human knowledge and how we acquire it. Hebb critiqued behaviorists for failing to recognize "that mind is itself, and always has been, simply a theory of behavior" and for overlooking a theory of mind based on the relation of the mind to things in the environment.²⁹⁰ Hebb questioned the philosophy of idealism's demand for making a distinction between the activities of bodies with the activities of minds, and cautioned against attributing to the mind an agency whose activities can account for human activity.

In the margins of Hebb's manuscript, the American philosopher Warner Wick (1911-1985), then a graduate student at the University of Chicago, handwrote references to the American sociologist George Herbert Mead's (1863-1931) *Mind, Self and Society* as relevant to Hebb's epistemological project. Beginning at the turn of the century, Mead took the idea of an individual's relationship to the environment in a different direction than his pragmatic colleagues who focused on knowledge and construction of the individual self. Mead denied the dominant conception of the self as individual. He said psychology should look to behaviors to understand the *expression* of consciousness and should not be concerned with the nature of consciousness because we cannot separate a self from its interaction with other selves.²⁹¹ Hebb, who said that attending to behavior and physiological activity was sufficient for constructing a theory of mind by elucidating the interaction of our inner world with the outside world, paralleled Mead's insistence that an understanding of mind depends only on understanding objects and how people act on them.

²⁹⁰ Typescript of "Scientific Method in Psychology: A Theory of Epistemology Based on Objective Psychology," 1933-1934, 0000-2364.01.191, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 22.

²⁹¹ Mead, George Herbert. "The Genesis of the Self and Social Control." *International Journal of Ethics*, 35;3(1925):251-277. See also, Mead, George Herbert. *Mind, Self and Society from the Standpoint of a Social Behaviorist*. Edited by Charles W. Morris. Chicago: The University of Chicago Press, 1934.

Recruited to the University of Chicago by Dewey, Mead drew from Wundt's concept of the vocal gesture when formulating his conception of the social self. Mead also was shaped by the Hegelian dialectic and the evolutionary perspective and functional pragmatism of Dewey and James, the latter having traveled to Germany in the 1860s to study with Wundt and Helmholtz.²⁹² Mead framed the self as a sociological project, leading to the sociological denial of the self as individual. Mead said that all psychological activity has social content, including perception and emotion. The inner self is therefore an expression of the social self. We act based on how we interpret each other's gestures, said Mead; there is no self without interaction. Thus, Mead was concerned with creating a social psychology which integrated the social acts that led to the formation of the self.²⁹³ Mead's work departed from his fellow pragmatist James, who described the stream of consciousness as a continuum of an individual's experiences or thoughts linked over time, but it also acted as a bridge between James' pragmatic tradition and American sociology.

Mead's idea that the self is formed through a process of socialization, and that the way people socialize changes over time and place, was shaped also by the philosophy of Frenchman Henri Bergson (1859-1941) and the behaviorism of Watson. According to Mead, behaviorist psychology was not responsible for the content of the objects; it was interested in physiology and dynamics, and was thus not concerned with epistemology. Mead described behaviorism as caring only about processes, or with actions related to objects. Thus, according to Mead, behaviorist psychologists turned to the central nervous system as the material "dumping-ground" of

²⁹² Smith, Roger. "Shaping Psychology." In *Between Mind and Nature: A History of Psychology*, 70-101. London: Reaktion Books, 2013; Mandler, George. "The Birth of Modern Psychology: Wilhelm Wundt and William James." In *A History of Modern Experimental Psychology: From James and Wundt to Cognitive Science*, 51-75. Cambridge, MA: The MIT Press, 2007.

²⁹³ Mead, George Herbert. "The Genesis of the Self and Social Control." *International Journal of Ethics*, 35;3(1925):251-277.

consciousness; they stopped caring about consciousness and where it lies. But for Mead, the question remained: how do we regard the expression of consciousness? He thought Bergson's theory of perception was a step in the right direction—as far as the content of perception is recognized as consciousness, it indicates a diminution of the reality of the object rather than an addition, and this diminution answers to the active interests of the organism; a percept is a distortion of reality, not a reflection of it.

Following from pragmatism, Mead did not use the word consciousness in the sense of "awareness"; for Mead, consciousness referred to sensing the quality of things, the feelings of the body, the contents of images of memory and imagination, and the activities of the organism, all of which are created as an object and individual interact and relate with each other. Objects become social when they obtain an objective meaning to members of a group; imagery (interpretation) and meaning (definition) are the contents of objects which appear before the mind before an individual interacts with that object, he said. The imagery and meaning of objects, furthermore, are plastic and can change historically, and so can social acts. Consciousness, therefore, has an historical component to it. Mead drew from Bergson's philosophy of change—which conceived of life (and time) as a process and not a series of static physicochemical situations—and interpreted experience as conduct or behavior, not as a series of conscious states. Mead therefore traced how the self and the mind arise through the individual and the object interacting with each other.²⁹⁴

Bergson rejected that the past could be located in the brain. The brain, according to Bergson, acts like a throughway to connect us to the past; maladies of memory are disturbances in our link to the past, not destructions in the material engram in the brain. Bergson reacted to

²⁹⁴ Mead, George Herbert. "The Genesis of the Self and Social Control." *International Journal of Ethics*, 35;3(1925):251-277.

what he received as a material analysis of the brain and its functions with an idea that he could redeem anti-reductionism with an epistemology of more than the sum of its parts. Articulating a conceptualization of active and passive memory as incessantly contextualized, Bergson stressed the interrelation and constant dialogue between the mind with the functionality of the brain which only intuition could reveal.²⁹⁵ Bergson also said that through a process of active reconstruction of experiences from the past—creative evolution—memories serve the purpose of maintaining cohesion and continuity in consciousness. Through his philosophy, Bergson clearly articulated of the temporal component of memory and its relation to identity while critiquing Kant who said that human freedom existed outside of space and time.²⁹⁶

Mead critiqued Bergson for the latter's inability to explain the vital force and for ignoring that objects are things-in-themselves. For Mead, the world "out there" is a precondition for consciousness; he sided with the English philosopher Alfred North Whitehead (1861-1947) and against Bergson, that objects themselves can have some interpenetration, a reality to them, which science can reveal. By grounding human experience in action, Mead replaced metaphysics with a materialist theory of human action (i.e., behavior) as the basis of human experience, consciousness and social organization. Mead believed his social behaviorism moved beyond Watson's behaviorist psychology which only cared about actions in reaction to an object; Mead instead envisioned human behavior as part of a feedback loop mechanism which (re)creates

 ²⁹⁵ Roth, Michael, S. "Remembering Forgetting: Maladies de la Memoire in Nineteenth-Century France."
 Representations, Special Issue: Memory and Counter-Memory, (1989):49-68; Bergson, Henri. *Matter and Memory*. Translated by Nancy Margaret Paul and W. Scott Palmer. New York: The Macmillan Company, 2005, pp. 9-16.
 ²⁹⁶ Vaughan, Michael. "Introduction: Henri Bergson's Creative Evolution." *SubStance*, 36;3(2007)7-24; See also, Bergson, Henri. *Creative Evolution*. Translated by Arthur Mitchell. New York: Henry Holt and Company, 1911; Bergson, Henri. *Time and Free Will: An Essay on the Immediate Data of Consciousness*. Translated by F. L. Pogson. New York: The MacMillan Company, 1913. William James discussed Bergson's influence on him in *A Pluralistic Universe*. Edited by Ralph Barton Perry. New York: E. P. Dutton, 1909.

meaning through interaction. As a result, social control becomes a matter of self-control, opening up a possibility for changes in human behavior to lead to changes in social organization.²⁹⁷

Besides for Wick's reference to Mead in his notes on Hebb's 1934 epistemology essay, the direct influence of Mead on Hebb is likely minimal. Hebb's insistence on attending to human activity, however, reveals their parallels. An objective psychology, said Hebb, would use a theory of mind that combined subjective and objective methods toward the study of human activity as a whole. He cited the German Gestalt psychologist Wolfgang Köhler's (1887-1967) work with apes as an example of objective results vindicating introspective findings.²⁹⁸ Between 1913-1917 Köhler developed naturalistic experiments to make interpretations about the intelligence of apes. His work revealed, for example, that apes could use tools creatively in order to retrieve hard-to-access food, a solution which demonstrated to Köhler that apes possess intelligence and insight.²⁹⁹

In Germany, Gestalt psychology and its focus on perceptual generalization by the nervous system arose as a collaboration between the Austro-Hungarian-born psychologist Max Wertheimer (1880-1943), German psychologist Kurt Koffka (1866-1941) and Köhler before World War I, a time when a shift toward modernity and industrialization alarmed the cultural elite. Concerned less than their U.S. counterparts with using psychology to advance social progress than with the philosophical grounding of psychology as a study of what it means to be human, the three psychologists were part of a philosophical turn toward privileging "the

²⁹⁸ Hebb might have completed this manuscript after moving to Chicago to work with Lashley. It contains handwritten notes by then-graduate student in philosophy at the University of Chicago, Warner Wick. Typescript of "Scientific Method in Psychology: A Theory of Epistemology Based on Objective Psychology," 1933-1934, 0000-2364.01.191, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.
 ²⁹⁹ Köhler, Wolfgang. "Introduction." In *The Mentality of Apes*, 1-9. Translated by Ella Winter. New York:

²⁹⁷ Mead, George Herbert. "The Genesis of the Self and Social Control." *International Journal of Ethics*,
35;3(1925):251-277; Chasin, Gerald. "George Herbert Mead: Social Psychologist of the Moral Society." *Berkeley Journal of Sociology*, 9(1964):95-117.

Harcourt, Brace and Co., 1925.

phenomenon" as the way toward understanding how we come to know ourselves and the world.³⁰⁰ Köhler brought out the link between experiment and philosophy through a psychology of wholes which emphasized biological and physical concepts. Shaped by the German physicist Max Planck's (1858-1947) contributions to quantum physics and the idea that the distribution of discrete quanta of energy can be seen as a dynamical (i.e., as interacting forces affecting motion) and geometrical problem, Köhler argued that the human mind perceives the world not in bits and pieces through atomistic sensory elements, but as wholes, patterns, configurations, or *Gestalten* dynamically distributed through a perceptual field in meaningful topographical arrangements. In accordance with the theory of perceptual generalization of wholes as more than the sum of its parts, Köhler argued against behavioristic psychology which denied the perceptual process as fluidly interactive and organized as a functional whole and instead assumed local, isolated and stably connected pathways as the basis of sensory experience.³⁰¹

For Köhler, insight was the result of direct dynamical determination of physiological processes occurring in the brain field which correspond to and underlie the experienced whole. Distinct and relative features of the environment coalesce into experienced wholes through dynamically interacting physiological processes. According to Köhler, existing processes of the

³⁰⁰ Smith, Roger. "Varieties of Science." In *Between Mind and Nature: A History of Psychology*, 137-170. London: Reaktion Books, 2013; For a discussion of the relation between and reception of Gestalt psychology by phenomenological philosophers shaped by Franz Brentano's theory of parts and wholes and expressed by Edmund Husserl and Maurice Merleau-Ponty, see Heinämaa, Sara. "Phenomenological Responses to Gestalt Psychology." In *Psychology and Philosophy: Inquiries into the Soul from Late Scholasticism to Contemporary Thought. Studies in the History of Philosophy of Mind*, Vol 8. Edited by Sara Heinämaa and Martina Reuter, 263-284. Dordrecht: Springer, 2009. Heinämaa discussed how Gestalt-theorists focused on the structures of sense-perception and sensation whereas the phenomenologists attempted to ground a comprehensive theory of consciousness which accounted for all types of intentional acts and objects.

³⁰¹ Köhler, Wolfgang. "Dynamics Opposed to Machine Theory." In *Gestalt Psychology*, 103-147. New York: Horace Liveright, 1929. See also, Smith, Roger. "Shaping Psychology." In *Between Mind and Nature: A History of Psychology*, 70-101. London: Reaktion Books, 2013; Köhler, Wolfgang. "Gestalt Psychology Today." *American Psychologist*, 14;12(1959):727-734.

self can interact with incoming sensory processes, mediating experience. Similarly, sensory processes can determine properties of the physiological self:

As in experience I am surrounded by the things and events of my environment, so the processes corresponding to my self will be in the midst of a corresponding environment, consisting of sensory processes and so forth, in the brain field...Where, in dynamical determination, the properties of one part of a field depend directly upon the actual nature of some other particular part, those properties do not exist indifferently as such; they originate and they are maintained by the stress of just those particular forces which issue from the determining part, according to its actual nature. Assuming that the same is true in the brain field which is true in the physical field, the properties of the actual physiological self will change and may be kept changed awhile, under the stress of some particular process in the same field, corresponding to an essential thing or event in the experienced environment. The changed state of the self does not exist independently; it is produced and maintained by something definite, the actual nature of which expresses itself in just this dynamical influence.³⁰²

The holism of Gestalt psychology, which was well established in Germany by 1920, gathered a warmer reception in Europe than in the U.S., where focused remained on the atomistic approach of behaviorism. Gestalt psychology was embraced by many North American psychologists, however, and especially after several Gestaltists, many of whom were Jewish, had emigrated to the U.S. by the 1930s, Gestalt ideas began to seep into the mainstream of North American psychology, as evidenced by the work of Hebb.³⁰³ The American psychologist Robert

³⁰² Köhler, Wolfgang. "Insight." In *Gestalt Psychology*, 349-394. New York: Horace Liveright, 1929, pp. 374-375.
³⁰³ Sokal, Michael M. "The Gestalt Psychologists in Behaviorist America." *The American Historical Review*, 89;5(1984):1240-1263; Mandler, Jean Matter, and George Mandler. "The Diaspora of Experimental Psychology:

The Gestaltists and Others." In Perspectives in American History, Vol. 2, 371-419. Cambridge, MA: Charles Warren

Leeper (1904-1986), in a published attempt to show "The Relation between Gestalt Psychology and the Behavioristic Psychology of Learning" described Köhler's conceptualization of insight, or the "recognition by the subject of the relationships of different perceived objects," as "merely the end result of learning."³⁰⁴ Leeper's explanation ignored Köhler's insistence on the principles of physiological organization which allowed for flexible nervous processes, organized as *sets* depending on the relevant aspects of the stimulus—including those determined by inherited as well as acquired arrangements—to shape sensory experience.³⁰⁵

Despite Köhler's contributions, however, Hebb derided the denial by Köhler and Bertrand Russell that behavioral observations are objective and their corresponding insistence that observations represent a subjective perception of an objective entity. Hebb wanted to consider observations of events as objective; he rejected the epistemological assumption that true objectivity must be based in a physical entity.³⁰⁶ In trying to solve the problems of epistemology, therefore, the methods of an objective psychology must look for "the simplest instance" of the kind of mental activity which helps us understand human activity and "the part it plays in

Center for Studies in American History, Harvard University, 1968; Porter, Theodore M., and Dorothy Ross (eds.). *The Cambridge History of Science, Vol. 7. The Modern Social Sciences*. Cambridge: Cambridge University Press, 2003, pp. 262-267.

³⁰⁴ Leeper, Robert. "The Relation Between Gestalt Psychology and the Behavioristic Psychology of Learning." *Transactions of the Kansas Academy of Science*, 34(1931):268-273, 269. For more on the Gestaltists' (underappreciated) influence on American psychology, including the work of Tolman and Lashley, see Mandler, Jean Matter, and George Mandler. "The Diaspora of Experimental Psychology: The Gestaltists and Others." In *Perspectives in American History*, Vol. 2, 371-419. Cambridge, MA: Charles Warren Center for Studies in American History, Harvard University, 1968; Sokal, Michael M. "The Gestalt Psychologists in Behaviorist America." *The American Review*, 89;5(1984):1240-1263.

³⁰⁵ Köhler, Wolfgang. "Dynamics Opposed to Machine Theory." In *Gestalt Psychology*, 103-147. New York: Horace Liveright, 1929. See also, Köhler, Wolfgang. *Dynamics in Psychology*. New York: Liveright, 1940.
³⁰⁶ On page 37A, Hebb quoted Russell, Bertrand, *Philosophy*. New York, Norton, 1927, p.134: "To be specific, when Dr. Watson watches rats in mazes, what he knows, apart from difficult inferences, are certain events in himself. The behavior of rats can only be inferred by the help of physics, and is by no means to be accepted as something accurately knowable by direct observation;" Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

relation of man to his environment."³⁰⁷ In 1949, fifteen years later, Hebb would declare in his famous *The Organization of Behavior* this simplest instance of mental activity to be the cell assembly.

With a 1951 letter to Leeper, Hebb sent along a copy of his recently accepted manuscript, "The Role of Neurological Ideas in Psychology." The paper, intended as a chapter in *The Organization of Behavior*, was ultimately omitted from final publication, but was "now dragged out again."³⁰⁸ Hebb made a case for the role of theory in the interpretation of neurophysiological data and for the importance of including physiological facts into theories of psychology. He also noted that the "intervening variables" psychologists use to explain the "connections or 'autonomous' central processes (i.e., ones that do not depend moment to moment on any particular sensory stimulation)" were actually neural and physiological in nature.³⁰⁹ The paper, Hebb told Leeper:

> represents a longtime project – an adaptation to the 1950 situation of a paper that was first written in 1930-1934 (more than a paper, really, a first draft of an opus on the psychology of thinking <u>and</u> on epistemology...The point is that my epistemological convictions, concerning "real" intervening variables, preceded my physiologizing; and that they did not follow because I happened to work with a physiological psychologist, Lashley...Surely your remark that "physiology cannot cast any vote" in psychology is empty-organism in its implications; and how can one arbitrarily throw away half one's evidence about the organism one is trying to understand? Of course, physiological theory

³⁰⁷ Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 64.

³⁰⁸ Donald Hebb to Robert Leeper, September 29, 1951, 0000-2364.01.20.1, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

³⁰⁹ Hebb, D. O. "The Role of Neurological Ideas in Psychology." *Journal of Personality*, 20;1(1951):39-55, p. 41. Hebb defended the concept of psychological "intervening variables" as an alternative to the stimulus-response conception of behaviorists.

cannot deny psychological fact, logically, but cannot physiological fact contradict psychological theory; and cannot physiological theory even influence psychological theory?³¹⁰

Hebb's epistemological project to defend the role of theory in physiological interpretation relied on uncovering the taken-for-granted assumptions fundamental to neurophysiology. In December 1934 Hebb submitted a term paper for an anatomy course which was adapted from his M.A. thesis. The paper, titled "The interpretation of experimental data on neural action," showcases his early interest in applying data from neurology and physiology to the study of behavior by psychologists. Hebb found that prospect to be extraordinarily difficult, however, as long as physiological investigators relied primarily on the nerve-muscle preparation and spinal preparations to form conceptions of neural activity based on phenomena observed in the isolated nerve. He acknowledged the present impossibility of studying the direct functional relationship between cells, but bemoaned that the "great majority of investigators" considered "the individual cell as more or less an independent unit affected only by those cells whose inhibitory or excitatory action is specific to it."³¹¹ This assumption, said Hebb, is exactly that—an assumption—which should be re-evaluated. Others, including Köhler and Lashley, had already critiqued the isolated and stable route assumption.³¹²

Studies of structure—anatomical, histological and embryological—combined with studies of the activity of segments (in the case of the decerebrated animal) or of the whole animal

³¹⁰ Donald Hebb to Robert Leeper, September 29, 1951, 0000-2364.01.20.1, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

³¹¹ Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

³¹² Köhler, Wolfgang. *Gestalt Psychology*. New York: Horace Liveright, 1929, pp. 142-143; Weidman, Nadine M. *Constructing Scientific Psychology: Karl Lashley's Mind Brain Debates*. Cambridge: Cambridge University Press, 1999, p. 132.

contributed to the conception of the reflex route, assumed to be composed of "relatively unchanging paths along which an excitation peripherally aroused is conducted," said Hebb.³¹³ This stable and specific route conception of the reflex arc, according to Hebb, helped scientists provide an explanatory mechanism for determinism at the neural level.³¹⁴

Hebb went on to recite prominent physiologists' interpretations which relied on the static route assumption. For example, in his 1929 Ferrier Lecture, Sherrington identified a phenomenon he termed "occlusion," found by experimenting with electrical stimulation of two afferent nerve fiber projections from the spinal cord which converge upon the same hindlimb muscle of cats. If he stimulated one nerve enough to elicit maximum muscle contraction, no further stimulation to the second nerve could excite a stronger muscular contraction (also referred to as "mechanical tension" or "contraction-tension" by Sherrington), resulting in what Sherrington called occlusion of excitation. Backed by histological evidence reported by Ramón y Cajal in 1903, Sherrington explained occlusion using the assumption that the two afferent nerves overlap and converge on the same motor units some point on the same stable structural path.³¹⁵ In his telling, Sherrington assumed the path of nerve transmission could *not* be changed by excitation from afferent impulses, indicating his adherence to the stable route concept.

³¹³ Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 2.

³¹⁴ Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 3.

³¹⁵ Sherrington defined "motor unit" and described spinal convergences: "One set of spinal convergences lies where the several afferent nerves which excite or inhibit a given muscle converge upon the mouth of the motor channel leading to that muscle. The muscle itself can serve as an index of the interaction. The muscle and its nerve may be thought of as an additive assembly of 'motor units,' (1) meaning by 'motor unit' an individual motor nerve-fibre together wth[sic] the bunch of muscle-fibres it activates. Each such 'motor unit' has centrally [i.e., in the central nervous system], of course, a nerve-cell of which a group or 'pool' represent the muscle in the spinal cord" (p. 333). Sherrington, Charles S. "Ferrier Lecture—Some Functional Problems Attaching to Convergence." *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 105;737(1929):332-362.

Hebb thought the stable reflex route assumption too rigid. He believed that physiological change—learning—resulting from an organism interacting with its environment did not have to occur along stable paths. He speculated that incoming excitement might be a factor in determining the *direction* of electrical transmission and thus be a mechanism for adaptation at the cellular level. In fact, German scientists had found such principles of functional adaptation at work in both invertebrates and vertebrates following renewed interest in the central nervous system's healing processes as large numbers of wounded veterans returned from World War I with brain injuries.³¹⁶ Hebb claimed it unlikely to be inhibitory action at work in the isolated nerve, especially considering Adrian and his American collaborator, physiologist Detlev Wulf Bronk (1897-1975), had ruled out the dual property of propagated disturbance upon abandoning the refractory-phase hypothesis in 1929.³¹⁷

The refractory-phase hypothesis arose as an attempt to explain Wedensky inhibition, the phenomenon that strong or rapidly recurring electric stimuli to a nerve fiber produces a small muscle contraction whereas weak or slowly recurring stimuli produces a continued tetanus (i.e., sustained contraction) of the muscle. According to the refractory-phase hypothesis, a refractory state—the short period after discharge in which a fiber cannot produce a second discharge—in one conducting path blocks the path of other impulses.³¹⁸ Adrian and Bronk showed that the discharge frequency from a sense organ (e.g., skin) closely parallels the frequency of a motor

³¹⁶ Hebb cited Bethe, Buddenbrock, Goldstein in Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada. Bethe's citation by Hebb is a chapter on "Plasticity and Localization Theory" (translated from the German "Plastizitaet und Zentrenlehre") from his 1931 textbook on experimental physiology *Handbuch der Normalen und Pathologischen Physiologie*. See also, Stahnisch, F. W. "From 'Nerve Fiber Regeneration' to 'Functional Changes' in the Human Brain—On the Paradigm-Shifting Work of the Experimental Physiologist Albrecht Bethe (1872-1954) in Frankfurt am Main." *Frontiers in Systems Neuroscience*, 10;6(2016):1-16.

³¹⁷ Adrian, E. D., and D. W. Bronk. "The Discharge of Impulses in Motor Nerve Fibres. Part II. The Frequency of Discharge in Reflex Voluntary Contractions." *The Journal of Physiology*, 67;2(1929):119-151.

³¹⁸ Adrian, E. D. "Some Recent Work on Inhibition." *Brain*, 47;4(1924):399-416.

nerve cell connecting to the sense organ, which was interpreted by Hebb as debunking the refractory-phase theory of inhibition along stable conductive paths.³¹⁹

Hebb went on to critique neurophysiologists' recourse to the stable route theory when attempting to explain the phenomenon of fatigue, both in muscles and nerves. Sherrington claimed the observation of muscular fatigue (i.e., a weakening, or relaxing, of contraction) as a result of inhibition from an afferent nerve converging on its effector muscle. The greater magnitude of fatigue, said Sherrington, occurs because an inhibitory stimulus (from the afferent nerve) "will act more powerfully, *i.e.*, will arrest more active units, when employed late in the course of the tetanic plateau than when employed early."³²⁰ Similarly, when describing the phenomenon of nerve fatigue, the American neurophysiologists Alexander Forbes (1882-1965) and Ralph Gerard (1900-1974) assumed an observed decrease in nerve excitability toward a new functional equilibrium as due to changes in the nerve's oxygen consumption and heat production, both of which presumably affect the ability of the nerve to discharge energy in the form of an electrical impulse.³²¹ Hebb, in contrast, stated that if neurophysiologists were not bound by their stable route assumptions, they might conceive the effect "be because of an increased tendency to activate other neurons than the ones studied," resulting in a "consequent re-distribution of excitation" which takes "another avenue of discharge."322 Later, in The Organization of Behavior, Hebb insisted that, "'[e]xcitation,' 'inhibition,' and 'fatigue,' as prolonged neural

³¹⁹ Adrian, E. D., and D. W. Bronk. "The Discharge of Impulses in Motor Nerve Fibres. Part II. The Frequency of Discharge in Reflex Voluntary Contractions." *The Journal of Physiology*, 67;2(1929):119-151; Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

³²⁰ Sherrington, Charles S. "Ferrier Lecture—Some Functional Problems Attaching to Convergence." *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 105;737(1929):332-362, p. 354.

³²¹ Forbes, Alexander. "The Mechanism of Reaction." In *A Handbook of General Experimental Psychology*. Edited by Carl Murchison, 155-203. Worcester, MA: Clark University Press, 1934; Gerard, Ralph. "The Activity of Nerve." *Science*, 66;1717(1927):495-499.

³²² Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 6.

conditions determining the behavior of the whole animal, are conceptions which perhaps are not a primary concern for the neurophysiologist but which certainly need examination in psychological theory."³²³ His critique of the Sherringtonian stable route theory, therefore, had to do with the theory's inability to materially account for psychological factors like learning, memory and emotion to shape an organism's behavior.

Hebb went on to critique Pavlov's notion of internal inhibition at work in the formative process of conditioned reflexes. Pavlov explained the extinction of conditioned reflexes as due to central inhibition (i.e., from the cerebral cortex) related to the "functional exhaustion of the cortical elements."³²⁴ Pavlov, said Hebb, "represents the most complete assumption of the linear passage of excitations along specific routes," assuming a point-for-point specificity of cortical excitation corresponding to excitation in the periphery.³²⁵ Pavlov, who in 1904 won the Nobel Prize for his work elucidating psychic factors at work in dogs' salivary secretion, maintained that the phenomena of conditioned reflexes could help physiologists uncover the complex structure and organization of the cerebral cortex. The concept of the conditioned reflex, furthermore, underpinned neobehaviorist connectionist theories of learning.³²⁶

According to Pavlov, the theory of reflex activity, based on the theory of localization of functions in the cortex, had support in three fundamental principles by which organisms learn to behave within their environment and are accessible by scientific investigation: determinism, analysis and synthesis, and structure. The principle of determinism assumed an appropriate and

³²³ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, p. 208.

³²⁴ Pavlov, I. P. *Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex.* Edited and translated by G. V. Anrep. Oxford: Oxford University Press, 1927, p. 246.

³²⁵ Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 7.

³²⁶ See e.g., Hull, Clark L. "Introduction to an Objective Theory of Behavior" and "Stimulus Reception and Organism Survival." In *Principles of Behavior: An Introduction to Behavior Theory*, 16-49. New York: Appleton-Century-Crofts, 1943.

reliable effect or action for a given cause. The principle of analysis and synthesis assumed that a whole can be decomposed into its corresponding parts or units; consequently, a whole can be reconstructed by learning about individual parts or units and piecing them back together. The principle of structure assumed a coherent distribution of activity in space, and that function adapts to the structure of the organism.³²⁷ For Pavlov, reflex theory was compatible with the idea that phenomena occurring in an organism are connected with the conditions that determine them; conditioned reflexes demonstrated the integrated activity of the organism and the importance of the complex organization of the cortex. Pavlov therefore believed that the task of neurophysiologists was to use reflex theory to understand associations between separate phenomena by linking them to the (as-yet-determined) complex organization and cytoarchitecture of the nervous system in order to fully understand an organisms' behavior. Hebb, in contrast, wanted to consider alternatives to understanding the relationship between behavior and cerebral activity, like ones that did not assume "a separate specific cortical excitation corresponding to each peripheral excitation, but a diffuse excitation of which a large fraction might be common to two or more peripheral excitations," which could be narrowed down only through a process of differentiation.³²⁸ Later, in his famous *The Organization of* Behavior, Hebb detailed the inadequacies of Pavlovian conditioning theory and presented his form of association theory which attempted to repair the inadequacies of conditioning theory.³²⁹

For Pavlov, dynamic processes occur at the cellular level along defined paths in the brain. Pavlov advocated the idea that a conditioned response became associated with an unconditioned

³²⁷ Pavlov, I. P. "The Reply of a Physiologist to Psychologists." *Psychological Review*, 39;2(1932):91-127.

³²⁸ Typescript of "The Interpretation of Experimental Data on Neural Action," 1934, 0000-2364.01.188, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 7.

³²⁹ Donald Hebb to Henry Nissen, May 19, 1948, 0000-2364.01.6, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

stimulus as cortical excitation resulting from an unconditioned stimulus "irradiates" to the predetermined path of excitation evoking a particular conditioned response, which must be spatially located within the field of excitation of the unconditioned response.³³⁰ As a result, Pavlov critiqued the experimental interpretations of Lashley, which to Lashley demonstrated diffuse cortical activity, disproved localization theory, and implied the nervous system's innate capacity for the functional organization of behavior which did not rely on a strict correlation between function and the variegated structure of the cortex.³³¹ For Lashley, the cortex did more than the coordination of reflexes; its complexity came from something more than its complex cytoarchitecture.³³²

Lashley attacked the behaviorist brand of connectionism, instead insisting on a strict biological approach to a psychological analysis of brain function. Lashley advocated for the heredity of intelligence, opposing environmentalist and localization of function arguments.³³³ His extirpation of cortex experiments in rats and monkeys provided evidence of the diffuseness of intelligence; Lashley found that the total amount—not which part—of cortex removed affected performance in discrimination and problem-solving behavior. His "law of mass action" and "law of equipotentiality" of the brain served as evidence for the heredity of intelligence and affirmed his stance in the nature-nurture debate. He found an ally in Spearman, who was interested in

³³⁰ The Russian American psychologist Gregory Razran claimed that through personal communication with Pavlov in 1934 he understood Pavlov to be well versed in the writings of Wundt, James and the British Associationists but had little understanding of contemporary American psychology. Razran said also that the teachings of Pavlov and his disciple Bekhterev were considered amongst Russians as insufficiently Marxist (i.e., they were materialistic, but not dialectical enough). Razran, Gregory. "Stimulus Generalization of Conditioned Responses." *Psychological Bulletin*, 46;5(1949):337-365; Lashley, K. S. and M. Wade. "The Pavlovian Theory of Generalization." *Psychological Review*, 53;2(1946):72-87.

 ³³¹ Pavlov, I. P. "The Reply of a Physiologist to Psychologists." *Psychological Review*, 39;2(1932):91-127.
 ³³² Lashley detailed his experiments and position in his only published monograph, *Brain Mechanisms and Intelligence: A Quantitative Study of Injuries to the Brain*. Chicago: The University of Chicago Press, 1929.
 ³³³ See e.g., Lashley, K. S. "Basic Neural Mechanisms in Behavior." *Psychological Review*, 37;1(1930):1-24; Lashley, K. S. "Coalescence of Neurology and Psychology." *Proceedings of the American Philosophical Society*, 84;4(1941):461-470; Lashley, K. S. "Cerebral Organization and Behavior." *Proceedings of the Association for Research in Nervous and Mental Diseases*, 36(1958):1-18.

finding the neurophysiological correlate of general intelligence (g) and had the view, according to Lashley, "that intelligence is a function of some undifferentiated nervous energy."³³⁴ For Lashley and Spearman, therefore, intelligence was not localized in particular regions, but was a unified entity, a property of the whole brain.

By the late 1920s Lashley, who was taught by Watson, had reversed course on believing in the reflex as underpinning all behavior and began to associate reflex connectionism with the doctrine of the localization of function.³³⁵ In 1929, during the Presidential Address to the American Psychological Association before the Ninth International Congress of Psychology in New Haven, Connecticut, Lashley, stressing the need to account for behavior in terms of nervous processes, objected to the idea of cerebral localization of function and the theory of nervous integration achieved through a complex hierarchy of reflex arcs. He said that attempting to understand the activity of individual cells along definite paths will not give us a complete picture of brain functioning; what matters, he said, is the "relational framework" between excited parts of the cortex which can influence each other in some way.³³⁶ Lashley thus denied that the environment entirely shaped behavior, insisting instead that the central nervous system acted independently to control behavior.

³³⁴ Lashley, K. S. "Basic Neural Mechanisms in Behavior." *Psychological Review*, 37;1(1930):1-24, p. 16. See also, Lashley, K. S. *Brain Mechanisms and Intelligence: A Quantitative Study of Injuries to the Brain*. Chicago: The University of Chicago Press, 1929; Weidman, Nadine M. "Neuropsychology and Hereditarianism" and "Intelligence Testing and Thinking Machines: The Lashley-Hull Debate." In *Constructing Scientific Psychology: Karl Lashley's Mind Brain Debates*, 71-83, 128-142. Cambridge: Cambridge University Press, 1999.

³³⁵ Weidman, Nadine M. "The Pursuit of a Neutral Science" and "Neuropsychology and Hereditarianism." In *Constructing Scientific Psychology: Karl Lashley's Mind Brain Debates*, 48-83. Cambridge: Cambridge University Press, 1999.

³³⁶ Lashley suggested scientists look to experimental embryology because of similarities of growth and development with nervous function; nervous activity might be modified by influences such as gaseous interchange, chemical diffusion, metabolic activity, or electrical polarization, for example. Lashley, K. S. "Basic Neural Mechanisms in Behavior." *Psychological Review*, 37;1(1930):1-24.

Lashley's support of whole-brain functioning over the localization of function aligned with Gestalt psychologists' holistic conception of mind as patterns and sequences of reactions and interactions.³³⁷ Although Lashley's focus on the internal, biological correlates of behavior was against the behaviorist insistence that science could only properly examine inputs and outputs (i.e., the external manifestation of biology), he wrote to Hebb in 1949, following publication of *The Organization of Behavior*, that he was "deeply offended at being classed a gestalt psychologist, since I consider myself the only surviving behaviorist."³³⁸ His doctrine of equipotentiality and mass action, to him supporting the notion of intelligence as a unified entity, however, placed Lashley firmly against learning psychologists like Pavlov and Hull who reduced intelligence to many psychological constituents, corresponding to a mosaic of neurological processes functioning independently.³³⁹ Lashley's debates with behaviorists linked the mindbody debate with the nature-nurture debate through studies of intelligence and learning. Hebb attempted to resolve their differences with his neuropsychological theory which acknowledged the importance of autonomous central processes but also introduced a way for electrical activity to change their structure.

Attempting to reconcile the nature vs. nurture debate

In the concluding pages of *The Organization of Behavior*, under the subtitle "The Nature and Nurture of Intelligence," Hebb declared "that there is a major effect of experience on the

³³⁷ Lashley, K. S. "The Behavioristic Interpretation of Consciousness - I and II." *Psychological Review*, 30;4&5(1923):237-272, 329-353.

³³⁸ Karl Lashley to Donald Hebb, November 22, 1949, 0000-2364.01.195, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.

³³⁹ Weidman, Nadine M. "Intelligence Testing and Thinking Machines: The Lashley-Hull Debate." In *Constructing Scientific Psychology: Karl Lashley's Mind Brain Debates*, 128-142. Cambridge: Cambridge University Press, 1999; Pavlov, I. P. "The Reply of a Physiologist to Psychologists." *Psychological Review*, 39;2(1932):91-127; Lashley, K. S. and M. Wade. "The Pavlovian Theory of Generalization." *Psychological Review*, 53;2(1946):72-87.

IQ.³⁴⁰ He acknowledged two separate meanings of intelligence, one that depended on innate potential, and another that revealed "the actual level of comprehension, learning, and problem-solving *in this culture*."³⁴¹ Engaging with the nature vs. nurture debate, Hebb went on to assert that "[t]here are then two determinants of intellectual growth: a *completely necessary* innate potential...and a *completely necessary* stimulating environment. It is not to the point to ask which is more important."³⁴²

The final words of the book make clear that, unlike his teacher Lashley, Hebb viewed the discipline of psychology as instrumental in promoting individual intellectual development and social progress:

Schooling also is becoming more and more necessary to an understanding of adult problems in this society, and a certain amount of wealth, of freedom from economic pressure, may be quite necessary to full intellectual development. The fact is, however, that we know almost nothing specific about the matter. The country may be full of potential geniuses, for all we know, and it should be a pressing concern for psychology to discover the conditions that will develop whatever potentialities a child may have.³⁴³

That Hebb thought psychology could discover the conditions that would improve intellectual development reflected his confidence in the malleability of the mind and reveal his sympathies with the pragmatic principles of James, Dewey and Mead. His postdoctoral work with the neurosurgeon Penfield also solidified his belief in the cortical diffuseness of intelligence

³⁴⁰ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, p. 299.
³⁴¹ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, p.

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³⁴² Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, p. 302.

³⁴³ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, p. 303.

and against its localization, which to Lashley attested to its innateness. Between 1937 and 1939 Hebb worked with Penfield at the Montreal Neurological Institute, studying the effects of bilateral frontal lobe operations upon human intelligence.³⁴⁴ At the time, the prevailing view was that the frontal lobes were especially important for intelligence and personality. "By early 1938," said Hebb, however, "it was clear that the relation of brain and intelligence, in man, was quite different from what it was supposed to be."³⁴⁵ Hebb and Penfield found clean removal of the frontal cortex to have minimal effect on intelligence as measured by standardized tests like the Stanford-Binet test.³⁴⁶ As a result, Hebb argued against the interpretation of famed American lobotomists, the physician Walter Freeman (1895-1972) and neurosurgeon James Watts (1904-1994), who declared the frontal lobes as critical to temperament and the capacity for foresight; Hebb asserted instead that "social and intellectual defects need not follow" from surgical excision of frontal lobe tissue.³⁴⁷

Beginning in 1944, Hebb, sympathetic to Köhler's *Gestalt Psychology* and Lashley's critique of reflex theory, but also accounting for Pavlov and Hull's theory of the structural stimulus trace as the basis of memory, set out to reconcile these seemingly irreconcilable differences, after his research experience with Penfield made him reconsider that neural tissue

³⁴⁴ Brown, Richard E., and Peter M. Milner. "The Legacy of Donald O. Hebb: More than the Hebb Synapse." *Nature Reviews Neuroscience*, 4(2003):1013-1019; Hebb, D. O. "A Neuropsychological Theory." In *Psychology: A Study of a Science, Study I. Conceptual and Systematic. Volume 1. Sensory, Perceptual, and Physiological Formulations.* Edited by Sigmund Koch, 622-643. New York: McGraw-Hill, 1959.

³⁴⁵ Hebb, D. O. "A Neuropsychological Theory." In *Psychology: A Study of a Science, Study I. Conceptual and Systematic. Volume 1. Sensory, Perceptual, and Physiological Formulations.* Edited by Sigmund Koch, 622-643. New York: McGraw-Hill, 1959, p. 624.

³⁴⁶ Hebb, D. O. "Intelligence in Man After Large Removals of Cerebral Tissue. Report of Four Left Frontal Lobe Cases." *The Journal of General Psychology*, 21(1939):73-87; Hebb, D. O., and W. Penfield. "Human Behavior After Extensive Bilateral Removal from the Frontal Lobes." *Archives of Neurology and Psychiatry*, 44;2(1940):421-438; Hebb, D. O. "Man's Frontal Lobes: A Critical Review." *Archives of Neurology and Psychiatry*, 54;1(1945):10-24.

³⁴⁷ Hebb, D. O. "Man's Frontal Lobes: A Critical Review." *Archives of Neurology and Psychiatry*, 54;1(1945):10-24, p. 24. Hebb referred to the interpretation by Freeman and Watts published in Freeman, W., and J. W. Watts. *Psychosurgery: Intelligence, Emotion and Social Behavior Following Prefrontal Lobotomy for Mental Disorders*, Springfield, IL: Charles C. Thomas, 1942.

responsible for intellectual development might not be necessary for its continued maintenance.³⁴⁸ Gestalt theory centered on the idea that perception was the act of comparing a figure to a ground; perception was not a reaction to an individual stimulus, but an active comparison of stimuli so that one stimulus or certain aspects of stimuli become dominant while others recede to the background. Experiments testing the perceived equivalence of stimuli supported the Gestalt concept of perceptual generalization [see **Figure 4.1**].

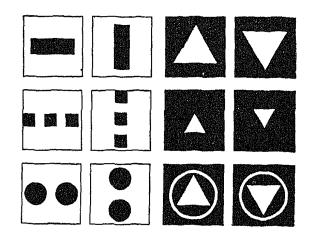


Figure 4.1: Example stimuli presented to rats to illustrate perceptual generalization.³⁴⁹

Figure 4.1 shows representative stimuli that Lashley presented to rats in his experiments on perception which demonstrated the phenomena of equivalence of stimuli.³⁵⁰ The fact that rats could learn to distinguish orientation (e.g., horizontal or vertical) of a group of geometric shapes despite their individual differences (e.g., three small squares or two medium-sized circles

³⁴⁸ Hebb, D. O. "A Neuropsychological Theory." In *Psychology: A Study of a Science, Study I. Conceptual and Systematic. Volume 1. Sensory, Perceptual, and Physiological Formulations.* Edited by Sigmund Koch, 622-643. New York: McGraw-Hill, 1959, pp. 624-625.

³⁴⁹ Reprinted from Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. 14.

³⁵⁰ See e.g., Lashley, K. S. "The Mechanism of Vision XV. Preliminary Studies of the Rat's Capacity for Detail Vision." *The Journal of General Psychology*, 19(1938):123-193.

arranged horizontally or vertically) between trials in order to obtain food or avoid punishment (like falling into a net) signaled to Lashley and the Gestalt psychologists that learning could not be dependent on fixed and invariable routes in the nervous system. There is no spatial representation of learning dependent on connections between cells, they said, instead a dynamic pattern or field of sensory excitation enabled perception.³⁵¹ These experiments by Lashley contributed majorly to Hebb's skepticism of Sherrington and Pavlov's adherence to the stable route theory of connections.

Lashley and the Gestalt field theory of perception, however, did not adequately allow for prior experience to shape perception, according to Hebb. He believed in the existence of autonomous central processes operating independently of incoming stimuli, but also understood the necessity for neural processes that allowed an organism to learn through its interactions with the environment. The ability to learn, thought Hebb, required a neural mechanism of memory. Hull described the stimulus trace hypothesis—a hypothesis of biological expectancy—as the assumption of a perseverative neurobiological process which followed the discharge of electrical activity stemming from stimulation and which persisted for seconds to minutes after its termination.³⁵² To Hebb, the behavioral evidence pointing to expectancy showed the stability of learning and indicated a potential neural correlate of ideation and a "recognition that responses are determined by something else besides the immediately preceding sensory stimulation."³⁵³ The stimulus trace hypothesis—a lasting neurobiological impression of the past—provided a

³⁵¹ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, pp. 12-16.

³⁵² Hull credited Pavlov for the idea. Hull, Clark L. *Principles of Behavior: An Introduction to Behavior Theory*. New York: Appleton-Century-Crofts, 1943, pp. 42, 46.

³⁵³ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. 5; Hebb, D. O. "A Neuropsychological Theory." In *Psychology: A Study of a Science, Study I. Conceptual and Systematic. Volume 1. Sensory, Perceptual, and Physiological Formulations*. Edited by Sigmund Koch, 622-643. New York: McGraw-Hill, 1959, p. 631.

way to think about the neural correlate of experience and learning in perception, and paralleled Bergson's notion of creative evolution as well as Mead's conceptualization of the formation of the self and the mind as a constructive process of interaction between the individual and the outside world (which includes other individuals).

Hebb's concept of the cell assembly, his contribution which had the most enduring effect on subsequent production of neuroscientific knowledge, helped him to conjoin psychology and physiology, linking behaviorist studies with neurophysiological studies of neurons and their and electrical potentials. The cell assembly represented the first stage of perception, when sensory events activated networks of cells which, as closed systems, continued to be active and reverberate after cessation of sensory events. Persistent activity by the cell assembly led to lasting synaptic changes between connected neurons, reinforcing its permanency as a pattern which would readily be reactivated in the future.³⁵⁴

Work in electroencephalography (EEG) confirmed continuous electrical activity of the nervous system even without the presence of stimuli. Lorente de Nó's work demonstrating growth at the synaptic knob presented evidence for the possibility of real structural change between connected neurons that reverberate together.³⁵⁵ Formation of the cell assembly occurred, said Hebb, when one cell excites a second and "repeatedly or persistently takes part in firing" the second cell, resulting in "some growth process or metabolic change" in one or both cells, thereby increasing the efficiency of the first cell to excite the second.³⁵⁶

³⁵⁴ Hebb, D. O. "The First Stage of Perception: Growth of the Assembly." In *The Organization of Behavior: A Neuropsychological Theory*, 60-78. New York: John Wiley & Sons, 1949. For a summary and refinement of the cell assembly concept, see also Milner, Peter M. "The Cell Assembly: Mark II." *Psychological Review*, 64;4(1957):242-252. Rosenblatt cited Milner's paper and Hebb's theory in his original paper presenting the perceptron (see chapter 5 of this dissertation).

³⁵⁵ Hebb, D. O. "The First Stage of Perception: Growth of the Assembly." In *The Organization of Behavior: A Neuropsychological Theory*, 60-78. New York: John Wiley & Sons, 1949.

³⁵⁶ Emphasis omitted. Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. 62.

The reverberatory activity, or trace, said Hebb, would induce lasting and stable cellular change in parts of the brain other than those directly involved in sensation and movement. According to the theory, perceptual integration occurred through the growth of cell assemblies which formed as individual cells which consistently activated together and as a result formed stronger synaptic connections. The cell assembly was Hebb's attempt to "physiologize" the psychological notion of associationism (or, connectionism) as the basis of learning and memory. Thus, he combined the Sherringtonian synapse with eighteenth-century associationism as well as the contemporary notion of connectionism espoused by Lashley and others while indirectly engaging with Mead's interactionism and Bergson's philosophy of change.

The cell assembly represented an idea, or a thought, as a pattern of neural activity. Hebb developed the concept of the phase sequence to account for streams of thought (or, patterns of brain activity) existing over time.³⁵⁷ Neurophysiological experiments had brought to light considerations of timing in nervous transmission as a variable affecting discharge of excitation.³⁵⁸ Part of Lashley's support for posing behavior as integration of activity patterns, not as resulting from local processes linking up a successive chain of reflexes, was that localization could not adequately account for the existence of temporally organized intracerebral processes.³⁵⁹ More a psychological construct informed by behavior data than the physiological construct of the cell assembly, the phase sequence represented a series of cell assembly actions. The cell assembly represented a momentary pattern of electrical brain activity, a phase in the sequence of activity that amounted to a thought process or behavior. Each phase in the phase

³⁵⁷ Hebb, D. O. "Perception of a Complex: The Phase Sequence." In *The Organization of Behavior: A Neuropsychological Theory*, 79-106. New York: John Wiley & Sons, 1949.

³⁵⁸ See e.g., Gasser, Herbert S. "The Control of Excitation in the Nervous System." *Bulletin of the New York Academy of Medicine*, 13;6(1937):324-348 and chapter 3 of this dissertation.

³⁵⁹ See also, Lashley, K. S. *The Neuropsychology of Lashley: Selected Papers of K. S. Lashley*. Edited by Frank A. Beach, Donald O. Hebb, Clifford T. Morgan and Henry W. Nissen. New York: McGraw-Hill, pp. 337-338. See also Lashley's "In Search of the Engram" in the same volume, pp. 478-505.

sequence, then, was a "link in the chain of the thought process" which interacted with other sequences, perhaps running in parallel or interfering with one another.³⁶⁰ Complete understanding of the phase sequence—the temporal organization of cell assemblies—amounted to the complete control of behavior and its temporal integration, according to Hebb.³⁶¹

Hebb formulated his neuropsychological theory of perceptual integration to reconcile perceptual generalization and the memory trace. It represented his attempt to deal with the thought process and perception in the framework of a theory of learning.³⁶² Informed by physiological evidence, *The Organization of Behavior* explained learning, motivation, and emotional disturbances as temporally integrated patterns of activity. The book showcased Hebb's belief in the importance of environment in shaping experience, but included a role for the central nervous system's innate organizational capacity.

Conclusion

Donald Hebb, recognized by contemporary neuroscientists as a crucial figure in the history of neuroscience because of his concepts of the cell assembly and the Hebbian synapse, developed his ideas through an insistence on using the methods of natural science to inform psychological theory. In the introduction to *The Organization of Behavior*, Hebb claimed modern psychology took for granted that "behavior and neural function are perfectly correlated."³⁶³ We can only infer another's feelings and awareness, he said, from what they *do*. These observable

³⁶⁰ Typescript of "The Evolution of Thought and Emotion." James Arthur Lecture, American Museum of Natural History, 1948, 0000-2364.01.70, Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada, p. 4.

³⁶¹ Hebb, D. O. "Perception of a Complex: The Phase Sequence." In *The Organization of Behavior: A Neuropsychological Theory*, 79-106. New York: John Wiley & Sons, 1949, p. 105.

³⁶² Hebb, D. O. "A Neuropsychological Theory." In *Psychology: A Study of a Science, Study I. Conceptual and Systematic. Volume 1. Sensory, Perceptual, and Physiological Formulations.* Edited by Sigmund Koch, 622-643. New York: McGraw-Hill, 1959, p. 639.

³⁶³ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. xiii.

events, furthermore, are determined by electrical and chemical events in nerve cells. As a consequence, therefore, Hebb maintained that the mind "can only be regarded, for scientific purposes, as the activity of the brain, and this should be mystery enough for anyone."³⁶⁴ Though underwritten by the electroconductive model of behavior validated by the neurophysiological investigations of Sherrington and his colleagues (and before them by du Bois-Reymond and Helmholtz), Hebb's notion of the mind was distinct from the Sherringtonian and Skinnerian purely materialist models of behavior. Shaped by pragmatism and the Hegelian influences on philosophical approaches to theories of mind and the self, Hebb's neuropsychological theory reframed the notion of the mind and the self as incessantly becoming, incessantly changing through the neurobiological processes of learning and remembering.

Hebb attempted to bridge neurophysiology and psychology with a general theory of behavior as the expression of cell assemblies—groups of cells that are active together—whose connections get strengthened through facilitation. Hebb, against the tide of behaviorist psychology, accepted "nonsensory influences on behavior" owing to the brain's continuous activity and reasoned that any activity in the brain arising as a direct result of a sensory stimulus must be influenced by "pre-existent activity;" therefore, "there really is a rational basis for postulating a central neural factor that modifies the action of a stimulus" through a sort of coincidence detection.³⁶⁵ The job of modern neurophysiology and anatomy, then, was to figure out how previous activity (i.e., "learned" activity) modified current activity in the brain.

From beginning of his career Hebb was concerned with figuring out the "right" way to understand human knowledge. For him, a truly objective and fruitful psychology would pay

³⁶⁴ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. xiv.

³⁶⁵ Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons, 1949, p. 7; Sejnowski, Terrence J. "The Book of Hebb." *Neuron*, 24(1999):773-776.

attention to all of human activity—including nervous activity—not just behavior. But he wanted to better blend psychology with physiology, to allow theorizing into neurophysiology and also to make psychology truly physiologically-informed.

He wanted to move beyond the idea assumed by Sherrington and Pavlov that there are stable reflex routes along which excitation in the form of electroconductivity must traverse. On this point he agreed with Lashley and the Gestaltists who said that the function of individual cells don't matter, rather the activity pattern of networks of neurons represent the meaningful information that the nervous system innately integrates. Hebb thought the nervous system could dynamically change its interactions by altering synaptic connections between groups of cells. On this point he agreed with the behaviorists, but critiqued their adherence to the stable route localization of function theory. He thought the routes themselves could change. His theory, an explicit attempt at reconciling the generalization of perception with the behaviorist theory of learning, maintained the existence of ideational processes which can occur in the absence of adequate stimuli and are reinforced through a cellular-level learning mechanism. These ideational processes might be understood as physiological analogies to the psychological notions of minded behavior which could be used to predict and control behavior advanced by James, Watson and others. Hebb agreed with James, Dewey, Bergson and Mead that the simplistic and reductive Skinnerian model of behavior which claimed to care only about input and output was a completely inadequate model of the self. Hebb's embrace of dynamic synaptic change allowed for a way to think about how minded behavior could occur neurobiologically. His theory also opened up a space for describing the mind as a record of individual and social history in which the neural correlates of learning and remembering reveal the writing and re-writing of the self as created through social and environmental interaction.

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Hebb's neuropsychological theory must be understood as part of the

heredity/environment debate transformed into the mind/body debate. Lashley and Köhler seemed to have proved connectionism through the chain-reflex theory was impossible, but Hebb could see no way of dealing with learning except in connections. Hebb arrived at the cell assembly solution which required learning during growth to establish connections. The *Organization of Behavior* thus incorporated Lashley and Köhler's insistence on the brain's innate organizational capacity with the behaviorist insistence on experience as located in the brain. His work on frontal lobe lesions with Penfield provided support that intelligence was diffusely organized throughout the brain.

After Hebb arose many physiological attempts at demonstrating learning effects and memory traces in the nervous system. In the early 1970s, Eric Kandel and his colleagues began work to mimic Pavlovian conditioning in *Aplysia* and by 1985 had shown that a simple behavior, the gill-withdrawal reflex, could be modified by learning.³⁶⁶ In 1973, workers from the Norwegian neuroscientist Per Anderson's (1930-2020) lab in Oslo demonstrated long-term potentiation (LTP) of groups of cells in the hippocampus of anesthetized rabbits; British neuroscientist Timothy Bliss (1940-) and Norwegian neuroscientist Terje Lømo (1935-) electrically stimulated one path of nerve fibers and observed an enhanced response in the downstream connecting cells up to ten hours after "conditioning."³⁶⁷ Following the Anderson lab revelations, workers flocked to study LTP and would eventually reveal key molecules involved

³⁶⁶ Kandel, Eric R. "Even a Simple Behavior Can Be Modified By Learning." In *In Search of Memory: The Emergence of a New Science of Mind*, 187-197. New York: W. W. Norton & Company, 2006.

³⁶⁷ Bliss, T. V., and T. Lømo. "Long-Lasting Potentiation of Synaptic Transmission in the Dentate Area of the Anaesthetized Rabbit Following Stimulation of the Perforant Path." *The Journal of Physiology*, 232;4(1973):331-356.

in LTP which trigger additional receptors to appear at the synaptic membrane, enhancing the synaptic potential response.³⁶⁸

Tracing the history of ideas which made Hebb's theory possible reveals how the neurobiological capacities for learning and memory have become so essential to understanding the nature of the relationship between brain and mind. Hebb's psychological understanding of brain functionality places the study of learning and memory not in the purview of neurophysiology *or* psychology, but as necessarily at the intersection of these disciplines. Furthermore, the intersection informs and is informed by cultural interpretations of learning and memory and how they relate to what it means to be human and to have agency. A purely reductive epistemology of learning and memory is therefore without meaning. Hebb's work reveals the self as constantly in a process of reconfiguration which must be put into context over place and time.

Hebb framed learning and memory as not just components of cognition, but as at the very core of nervous system functioning. His neuropsychological theory must be understood as following from the historical legitimization of the materialist electroconductive and physiological models of nervous system functionality represented by the works of du Bois-Reymond, Helmholtz, Sherrington, Adrian, Hodgkin and Huxley, and others. It also must be understood as incorporating psychological notions of learning as interaction and change as well as integrating contemporary philosophy of mind. According to Hebb's theory, the thought process is a behavioral expression of learning and memory at the level of the cell assembly. His integration of materialistic epistemologies of the brain with psychological theories of minded behavior soon formed the backbone of statistical and cybernetically-informed computational

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³⁶⁸ See e.g., Kandel, Eric R. "A Return to Complex Memory." In *In Search of Memory: The Emergence of a New Science of Mind*, 279-285. New York: W. W. Norton & Company, 2006.

models of the "becoming brain" as physiological models of cognition. Although cyberneticallyinformed conceptualizations of the self incorporated Hebbian principles into computational models of brain functionality, these models represent a return to a reductionist mechanistic philosophy grounded in neurophysiological explanation.

Chapter 5

From Wiener's cybernetics to a parallel distributed processing approach

This chapter traces the influence of cybernetics, statistical probability, and physics on computational modeling of brain functionality from the mid- to late twentieth century. As shown in the previous chapter, the midcentury cyberneticians, a highly interdisciplinary group, were not the first to realize the necessity for a broad intellectual scope in order to address the complexity of the physiology of thought and the physiology of the self. Twentieth-century neural models of cognition emanating from cybernetic discourse must therefore be understood as incorporating ideas from sociocultural imaginaries of individual and collective memory.

In 1925, the French philosopher and sociologist Maurice Halbwachs (1877-1945) theorized about memory and its relation to history and cultural identity. Informed by Henri Bergson and French sociologist Émile Durkheim (1858-1917), who conceived of the social group as a psychical unit, Halbwachs used a sociological analysis to say that individual memory is fragmentary and does not turn into collective historical memory until interaction with a group. There is a locus for memory in memorials and commemorations, he said, but the transition from group memory is done through an imaginary space—collective memory is socially constructed. For Halbwachs, the past is a social construction shaped by concerns of the present. Thus, collective memory is a constructive process as opposed to a retrieval process and is sustained by

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social and moral props. Furthermore, social organization provides the framework within which constructed collective memory must fit.³⁶⁹

In 1932, the British experimental psychologist F. C. Bartlett (1886-1969), citing the parallels in Halbwach's work, declared individual memory a constructive process. Bartlett followed from Hermann Ebbinghaus' experimental approach yet spurned the statistical methods of the English eugenicists Francis Galton and Charles Spearman, relying instead on observation and interpretation.³⁷⁰ In the 1980s, a cadre of cognitive scientists advanced a parallel distributed processing (PDP) approach to neural modeling, citing Bartlett as helping elucidate the understanding of memory as constructed.³⁷¹ The PDP research group followed from the cybernetic tradition of using statistical methods to turn uncertainty into prediction, reframing the human brain as a statistician, a stance some psychologists had adopted decades earlier.

Statistics rose to prominence in the nineteenth century and by the mid-twentieth century Western governments and large institutions had embraced probabilistic strategies for social applications. Actuarial thinking pervaded the construction of the modern welfare state; a socialization of risk seemed to offer individual benefits without a sacrifice of autonomy. After World War II, actuarial thinking seeped into everyday American life.³⁷² The statistical viewpoint positioned numbers as a strategy of communication, and statistical error theory, which involved

³⁶⁹ Halbwachs, Maurice. *On Collective Memory*. Edited, translated, and with an introduction by Lewis A. Coser. Chicago: The University of Chicago Press, 1992, pp. 37-83.

³⁷⁰ According to Bartlett, the jury was still out on the possibility of group memory. Bartlett, F. C. *Remembering: A Study in Experimental and Social Psychology*. Cambridge: Cambridge University Press, 1932, pp. v-vi, 7-13, 294-314.

³⁷¹ McClelland, James L. "Memory as a Constructive Process: The Parallel Distributed Processing Approach." In *The Memory Process: Neuroscientific and Humanistic Perspectives*. Edited by S. Nalbantian, P. M. Matthews, and James L. McClelland, 129-155. Cambridge, MA: The MIT Press, 2011. Wiener visited Bartlett at his psychological laboratory at Cambridge in 1947. Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, p. 23.

³⁷² Horan, Caley Dawn. *Actuarial Age: Insurance and the Emergence of Neoliberalism in the Postwar United States.* A dissertation submitted to the faculty of the graduate school of the University of Minnesota, 2011.

averaging out over large amounts of data instead of cherry-picking the best measurements, helped protect against claims of bias and became integral to a sense of precision and discipline in the physical sciences.³⁷³

Psychology as a discipline embraced the sense of rigor and certainty mathematical statistics could bring to the study of subjectivity. At the turn of the century, social psychologists trying to establish an epistemological framework as robust as the natural sciences relied on massive datasets generated from quantitative statistical studies to develop a concept of normalizing. By the beginning of the twentieth century, widespread social interest in intelligence quotient (IQ) testing in schools, workplaces, the justice system, and the military supported psychology's alignment with medicine and the idea of a "selection" of the self. Bolstered by values of the Progressive Era, psychology became part of the modernist project to make society humanely ethical, in part by promoting democratic principles.³⁷⁴ For example, as World War I approached, the discipline of psychology attached itself to the war effort. The concept of national character orientated U.S. psychology toward understanding and affecting important public issues, and there was a turn toward studying national character at home. Positioned as helping to serve the country, psychological theories and applications were linked with democratic politics on one hand, the concept of mental hygiene assumed human personalities as capable of making rational choices and negotiating the emotional pitfalls of freedom (the basic elements of

³⁷³ Porter, Theodore. "Objectivity and the Politics of Disciplines." In *Trust in Numbers: The Pursuit of Objectivity in Science and Public Life*, 193-216. Princeton: Princeton University Press, 1995.

³⁷⁴ Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996. See also, Smith, Roger. *Between Mind and Nature: A History of Psychology*. London: Reaktion Books, 2013.

democratic morale); on the other hand, it was only by preserving democratic institutions that the psychological professions could ensure their futures.³⁷⁵

Statistics as a mode of reasoning became so embedded in the field that psychologists in the 1950s began to talk about the mind as an intuitive statistician. They framed cognition as the spontaneous process of the mind applying error theory to understand cause and effect, to separate signal from noise.³⁷⁶ Around this time sociobiologists, shaped by the cybernetic adoption of statistical mechanics to explain communication and control as strategies of prediction, studied populations and individuals as part of structured information and energy flow.³⁷⁷

As the roster of the Macy Conferences make clear, cyberneticians understood the need to bring in the social sciences as well as epistemology and philosophy of mind to begin an interrogation of the science of communication and control as it relates to nervous system functionality. Composed of mathematicians, engineers, neurophysiologists, psychiatrists, psychologists, sociologists, and anthropologists, the group gathered to achieve the common goal of mathematizing teleology. Despite the involvement of anthropologists in the Macy Conferences, however, cybernetics was ultimately concerned with the complex modeling of interactive machines. Cybernetics, an antecedent to the neural models of cognition discussed in this chapter, was an interdisciplinary form of mechanistic philosophy that originated with and was framed by mathematical reasoning. Thus, the Hegelian model of incessant becoming that emerged from PDP neural models of cognition were at their core driven by mathematical analytical frameworks which simulated the self in terms of complex mechanistic activity.

³⁷⁵ Herman, Ellen. "The Dilemmas of Democratic Morale." In *The Romance of American Psychology: Political Culture in the Age Of Experts*, 49-82. Berkeley: University of California Press, 1995.

³⁷⁶ Gigerenzer, Gerd, and David J. Murray. *Cognition as Intuitive Statistics*. Hillsdale, NJ: Erlbaum, 1987, pp. xixiii; Porter, Theodore. "Objectivity and the Politics of Disciplines." In *Trust in Numbers: The Pursuit of Objectivity in Science and Public Life*, 193-216. Princeton: Princeton University Press, 1995.

³⁷⁷ Haraway, Donna. "The Biological Enterprise: Sex, Mind, and Profit from Human Engineering to Sociobiology." In *Simians, Cyborgs and Women: The Reinvention of Nature*, 43-68. New York: Routledge, 1991.

Though not detailed in this chapter, late twentieth-century explanations of human cognition resting on neurophysiological assumptions also must be understood as shaped by wartime endeavors to "crack the code" in order to decipher secret radio messages transmitted by Germany and its allies, as well as by postwar military investment in cybernetics, cognitive science, and artificial intelligence as part of "closed-world" political discourse focused on surveillance and containment of communism.³⁷⁸

Modeling intelligent behavior probabilistically

By the 1940s, when the field of cybernetics began to coalesce and computing machines were getting more powerful, the brain was understood by many scientists as a complexly organized organ of communication and control. Technological advances in telecommunications led scientists to adopt new language when describing how the brain works at a cellular level. Scientists interested in "experimental epistemology" incorporated neurophysiological insights into mathematical models designed to tackle questions of how the brain might hypothetically encode behavior through the field of cybernetics.³⁷⁹

The American neurophysiologists Alexander Forbes and Catharine Thacher observed electric currents in the sciatic nerves of cats and frogs with a valve amplifier in 1919.³⁸⁰ Forbes,

³⁷⁸ Edwards, Paul N. *The Closed World: Computers and the Politics of Discourse in Cold War America*. Cambridge MA: The MIT Press, 1996.

³⁷⁹ Warren McCulloch's "experimental epistemology" was based on his desire to construct a theory of how the brain creates and represents knowledge grounded in physiological data. In his 1960 Alfred Korzybski Memorial lecture, published under the title "What is a Number, that a Man May Know It, and a Man, that he May Know a Number?" in *General Semantic Bulletin*, 26-7(1960):7-18, McCulloch claimed to have inherited the tradition of experimental epistemology through his neurophysiological work on the functional (and topographical) organization of the nervous system at Yale with the Dutch neurophysiologist J. G. Dusser de Barenne who in turn inherited the tradition from the German pharmacologist and physiologist Rudolf Magnus.

³⁸⁰ I was unable to determine the birth and death dates of Catharine Thacher, one of the three women cited or mentioned in this dissertation. Bradley, J. K., and E. M. Tansey. "The Coming of the Electronic Age to the Cambridge Physiology Laboratory: E. D. Adrian's Valve Amplifier in 1921." *Notes and Records of the Royal Society of London*, 50;2(1996):217-228; Forbes, A. and C. Thacher. "Amplification of Action Currents with the Electron Tube in Recording with the String Galvanometer." *The Journal of Physiology*, 53;3(1920):409-471.

like many neurophysiologists of his time, thought the study of the individual neuron was key to understanding the action of the central nervous system. In a 1922 paper which Forbes' student, the American physiologist Hallowell Davis (1896-1992), declared in 1949 as "one of the foundations of the new science of *cybernetics*" and which apparently greatly influenced "Norbert Wiener and others who were interested in theoretical problems of organization and control," Forbes remarked on how the "machine-like regularity of the response" of the nerve signal stands in contrast to the "obscure functional capacities" of the gray matter of the brain.³⁸¹ Focusing on nervous system functionality and in thinking about individual nerve fibers' role in these "obscure functional capacities," Forbes distinguished nerve fibers from the brain's gray matter based on the purpose each serves using an analogy with a telephone system:

The nerve fiber apparently exists for the purpose of transmitting messages to remote parts, rapidly, economically and without modification. The central structure appears to serve as a junctional point where messages from many regions may be correlated, relayed and distributed to other regions. In this respect the fibers and centers may be likened to the wires and central offices, respectively, of a telephone system.³⁸²

The telegraph and telephone analogy had been used by many early twentieth-century neurophysiologists as an indication they viewed the nervous system as a system of information transmission. By 1926, Edgar Adrian frequently described nerve impulses in terms of their functional capacity, using words associated with information and communication (e.g.,

³⁸¹ Davis, Hallowell. "The Forbes 'School' of Neurophysiology at Harvard." *Electroencephalography and Clinical Neurophysiology*, 1;2(1949):139-140, p. 139; Fenn, Wallace O. "Alexander Forbes 1882-1965: A Biographical Memoir." *Biographical Memoirs*. Washington, DC: National Academy of Sciences, 1969, 113-141, p. 119; Forbes, Alexander. "The Interpretation of Spinal Reflexes in Terms of Present Knowledge of Nerve Conduction." *Physiological Reviews*, 2;3(1922):361-414, p. 361.

³⁸² Forbes, Alexander. "The Interpretation of Spinal Reflexes in Terms of Present Knowledge of Nerve Conduction." *Physiological Reviews*, 2;3(1922): 361-414, p. 361.

"messages," "signals," and "codes").³⁸³ In his 1932 *The Mechanism of Nervous Action*, Adrian declared "sensory messages" as "scarcely more complex than a succession of dots in the Morse Code."³⁸⁴ Twentieth-century neurophysiologists' articulation of nervous system functionality in this way represents their cooperation ushering in what the American mathematician, philosopher and cybernetician Norbert Wiener (1894-1964) called "the age of communication and control."³⁸⁵ Whereas nineteenth-century scientists harnessed energy for powering the steam engine using Newtonian mechanics, twentieth-century scientists would transform energy into information through statistical mechanics.³⁸⁶

Between 1946 and 1953 the cybernetics group met annually in New York to participate in a series of multidisciplinary conferences funded by the Josiah Macy Jr. Foundation. Shaped by the positivist tradition, the cyberneticians spent two days a year for a decade presenting to each other and discussing ideas for mathematizing purpose and constructing a new theory of causality.³⁸⁷ The group drew inspiration from the homeostasis model, which derived from the French physiologist Claude Bernard's (1813-1878) conception of the *milieu intérieur*.³⁸⁸ The physiological principle of homeostasis was well-suited to the needs of the cybernetic group as it contained the notions of regulation, organization, and feedback within a single concept. Bernard emphasized that organisms are stable, organized beings capable of modifying their internal

³⁸³ Garson, Justin. "The Birth of Information in the Brain: Edgar Adrian and the Vacuum Tube." *Science in Context*, 28;1(2015):31-52.

³⁸⁴ Garson, Justin. "The Introduction of Information into Neurobiology." Philosophy of Science, 70;5(2003): 926-

^{936,} p. 930; See also, Adrian, Edgar D. *The Mechanism of Nervous Action*. Philadelphia: University of Pennsylvania Press, 1932.

³⁸⁵ Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, p. 39.

³⁸⁶ Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, pp. 38-39.

³⁸⁷ Heims, Steve J. *The Cybernetics Group: Constructing a Social Science for Post-War America*. Cambridge, MA: The MIT Press, 1991, pp. 10-30.

³⁸⁸ Heims, Steve J. *The Cybernetics Group: Constructing a Social Science for Post-War America*. Cambridge, MA: The MIT Press, 1991, pp. 15-30, 164-166; Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, pp. 114-115.

environments in response to external stimuli. The organism itself maintains and controls the *milieu intérieur*, rousing internal processes to return it to a steady state in the face of changing outer circumstances. The adaptability of the organism, therefore, contributes to the fixity of the internal state, said Bernard. In 1929, the American physiologist Walter B. Cannon (1871-1945) coined the term "homeostasis" to refer to the regulation exhibited by the various organs of a living being working together to achieve inner stability. Cannon credited the process of evolution for conferring an organism the ability to maintain homeostasis. The harmonious functioning of an organism could only be achieved, he said, through biological organization and activity operating purposefully to reach a steady state. More evolved "higher animals" who achieved homeostatic regulation and "knowledge of the stability," said Cannon, could be compared "in relation to the less efficient arrangements operating in lower animals and also in relation to attempts at securing stability in social and economic organizations."³⁸⁹

In his influential 1948 book *Cybernetics: Or Control and Communication in the Animal and the Machine*, Wiener asserted the many similarities between a brain and a computing machine. Looking to combine biology with mathematics, Wiener pointed out that like the nervous system, modern machines receive and transmit information and can store information as memories for subsequent retrieval, thanks in part to their highly ordered organizational structure. Crucially, both machines and nervous systems can change their operating processes because of previously acquired information. In living beings we call this learning, said Wiener; consequently, machines can be taught to learn, too. In fact, he said, some machines already use past information to return to a steady state: thermostats, automatic ship-steering systems, selfpropelled and targeted missiles, anti-aircraft gunnery systems, and rapid computing machines.

³⁸⁹ Cannon, Walter B. "Organization for Physiological Homeostasis." *Physiological Reviews*, 9;3(1929):399-431, p. 427; See also, Cannon, Walter B. *The Wisdom of the Body*. New York: W. W. Norton & Company, 1932.

The essential principle in all control mechanisms—living or nonliving—said Wiener, is feedback. Be it a nervous system or a computer, anything capable of communication and control must possess the ability to adjust its output using information already acquired about past input-output relations through feedback.³⁹⁰

Bridging engineering, biology and mathematics, cybernetic computational models of cognitive processes challenged behaviorist conceptions of purpose and cognition stemming from the American academic psychology of John Watson and reframed by neobehaviorists like Edward Tolman.³⁹¹ In a paper published in 1943 but originally presented as an introduction to cybernetics at the 1942 Cerebral Inhibition meeting, also sponsored by the Josiah Macy Jr. Foundation, Wiener, together with the Mexican neurophysiologist Arturo Rosenblueth (1900-1970) and American mathematician and electrical engineer Julian Bigelow (1913-2003), expressed disappointment with experimental behaviorist psychology. They bemoaned that behaviorists cared only about input and output, ignoring the intermediary processes going on inside the nervous system. In the paper, Rosenblueth, Wiener, and Bigelow sympathized with Gestalt psychologists who cared more about how fields or symbols, pieces of information, actively combine into meaningful wholes in the brain.³⁹²

The historian, sociologist and philosopher Andrew Pickering argued the field of cybernetics grew up during a time when epistemological inquiry dominated philosophy of science. Cyberneticians, therefore, largely steered clear of ontological conjecture about the specific and complex nature of the brain. They recognized the brain as an acting machine which

³⁹⁰ Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: MIT Press, 1948, pp. 6-15. See also, Wiener, Norbert. *The Human Use of Human Beings*. Cambridge, MA: The MIT Press, 1950.

³⁹¹ Heims, Steve J. *The Cybernetics Group: Constructing a Social Science for Post-War America*. Cambridge, MA: The MIT Press, 1991, pp. 10-13, 201-205.

³⁹² Rosenblueth, Arturo, Wiener, Norbert, and Julian Bigelow. "Behavior, Purpose and Teleology." *Philosophy of Science*, 10;1(1943):18-24.

performed its special role of adaptation, while overlooking-or at least acknowledging the inaccessibility of knowing—the repertoire of specific physical realities that allowed these actions to occur.³⁹³ Rosenblueth, Wiener, and Bigelow, therefore, cared more about the functions the brain performed than its behavioral output, which could have been achieved via any number of functional processes (i.e., measuring behavior does not necessarily provide any understanding of function). The key to thinking about the meaning of behavior, said the trio, was to think about purpose; purposeful activity had to be guided by feedback loops, they said.³⁹⁴ Attendees of the cybernetics meetings also talked about Gestalt-like perception as part of the feedback loop during purposeful activity.³⁹⁵ The 1943 Rosenblueth, Wiener, and Bigelow paper was an outgrowth of the latter two's military work during World War II and Rosenblueth's suggestion that feedback mechanisms in purpose tremor could help them develop a theory of prediction for self-tracking anti-aircraft gunnery based on the target's motion and position. The group used statistical mechanics to create a general mathematical theory for predicting the future based on incomplete information about the past.³⁹⁶ Statistical mechanics provided a methodological way forward for a cybernetic epistemology concerned with functional processes in animals and machines and which acknowledged unknown and inaccessible elements that contributed to these processes.

³⁹³ Pickering argued that the second generation of cyberneticians, which are not dealt with in this dissertation, emphasized epistemology more than the first generation, which included W. Ross Ashby, who acknowledged interest in understanding the inside of the black box that is the brain. Pickering, Andrew. *The Cybernetic Brain: Sketches of Another Future.* Chicago: The University of Chicago Press, 2010, pp. 22-30.

³⁹⁴ Rosenblueth, Arturo, Wiener, Norbert, and Julian Bigelow. "Behavior, Purpose and Teleology." *Philosophy of Science*, 10;1(1943):18-24.

³⁹⁵ Heims, Steve J. "Gestalten Go to Bits, 2: Köhler's Visit." In *The Cybernetics Group: Constructing a Social Science for Post-War America*, 224-247. Cambridge, MA: The MIT Press, 1991.

³⁹⁶ Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, pp. 5-13; See also, Kay, Lily E. "From Logical Neurons to Poetic Embodiments of Mind: Warren S. McCulloch's Project in Neuroscience." *Science in Context*, 14;4(2001):591-614; Heims, Steve J. *John von Neumann and Norbert Wiener: From Mathematics to the Technologies of Life and Death*. Cambridge, MA: The MIT Press, 1980.

Considering that the scientific endeavor had not yet completed—and probably never would—a through exploration of every nook and cranny in the natural world, cyberneticians embraced the theory of probability as indispensable to their theories of communication and control. The philosopher of science Ian Hacking traced the nineteenth-century erosion of belief in universal causality beginning with an "avalanche of printed numbers" which paved the way for the development of probabilistic statistical laws.³⁹⁷ Mathematical statistics solidified as a field between 1890 and 1930, offering social and natural scientists a way to bypass unknown hidden variables and grapple with large amounts of observational and experimental data to explain complex phenomena.³⁹⁸ Acceptance of indeterminism in social science disciplines and the traumatic upheaval of World War I challenged the evolutionary notion of historical progress which dominated nineteenth-century social science and resulted in a shift from diachronic to synchronic explanatory approaches, shaping functionalist models based on metaphors of adaptation which often relied heavily on statistical techniques.³⁹⁹

The Austrian physicist and philosopher Ludwig Boltzmann's (1844-1906) contributions to statistical mechanics were crucial to future neural modelers who would use the idea of entropy as a measure of information. His resistance to probabilism and its implication of uncertainty in physics eventually gave way to his recognition of possible chance effects in thermodynamic processes toward the end of the nineteenth century. Formulated first in 1824 and expressed formally in the 1850s, the second law of thermodynamics explains heat loss in conversion to

 ³⁹⁷ Hacking, Ian. "The Argument." In *The Taming of Chance*, 1-10. Cambridge: Cambridge University Press, 1990.
 ³⁹⁸ Porter, Theodore. "Statistics and Statistical Methods." In *The Cambridge History of Science, Vol. 7. The Modern Social Sciences*. Edited by Theodore M. Porter and Dorothy Ross, 238-250. Cambridge: Cambridge University Press, 2003; See also, Porter, Theodore. *The Rise of Statistical Thinking: 1820-1900*. Princeton: Princeton University Press, 1986.

³⁹⁹ Ross, Dorothy. "Changing Contours of the Social Science Disciplines." In *The Cambridge History of Science, Vol. 7. The Modern Social Sciences.* Edited by Theodore M. Porter and Dorothy Ross, 205-237. Cambridge: Cambridge University Press, 2003.

mechanical work. It states that heat naturally flows from warmer to cooler gases or bodies, not the other way around. In other words, heat flow is a process with directedness and is not (naturally) reversible. The second law of thermodynamics thus presented an incompatibility with Newtonian mechanics, whose laws were time-symmetric and thus reversible. According to Newtonian mechanics, which was concerned with measuring changing positions and velocities of bodies and particles resulting from forces acting upon each other, the same results would be obtained working backwards or forwards through the equations.

In the 1860s and 1870s, the Scottish mathematical physicist James Clerk Maxwell (1831-1879) developed his study of what would soon be called Maxwell's demon in the midst of debates about whether the laws of thermodynamics validated the doctrine of mechanical determinism and thus threatened the possibility of human freedom. Enthused by the statistical methods used by social scientists to distribute human populations into groups based on age, education, race, etc., Maxwell realized he would never obtain exact measurements of the positions and velocities of all the millions of individual molecules present in a container of gas, but could apply statistical distribution techniques to a kinetic theory of gases to explain transfer of heat. Boltzmann added a mechanical perspective to the kinetic theory, demonstrating that the distribution of gaseous molecules approaches the most statistically probable state of energy distribution, maximizing entropy in a closed system. Entropy, the measure of disorder in a system, is maximized when a system reaches thermodynamic equilibrium (i.e., no transfer of heat energy). Maxwell's demon was a hypothetical being-perhaps the human will-that somehow knew the momentum and position of all particles in a closed system. The demon could decrease the entropy of a closed system by opening and closing a gateway between two sides of a container of full of particles, allowing fast particles through to one side and forcing slow

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particles to the other side, making one side warmer than the other. In order to achieve this task, Maxwell's demon would need to have complete information about all the particles in the system.⁴⁰⁰

At the beginning of the twentieth century, the American mathematician, engineer and physical chemist Josiah Willard Gibbs (1839-1903) elaborated on statistical mechanics as a deductive science, demonstrating the reconciliation of the second law of thermodynamics with classical Newtonian mechanics by allowing for some uncertainty about the state of a system due to changes occurring in the system over the course of time.⁴⁰¹ According to Wiener, in 1925 the German theoretical physicist Werner Heisenberg (1901-1976) replaced the quasi-Newtonian statistical mechanics of Gibbs, which reduced the time series to a thread of determinate states developing from each other over time, with a quantum mechanics in which the past does not dictate the future state, but "merely the distribution of possible futures of the system."⁴⁰² Wiener devoted the first chapter of *Cybernetics* to the French philosopher Henri Bergson's contributions pointing out that the reversibility of the Newtonian system does not faithfully represent what we actually experience through the course of time; time runs from an observable past to a future which can only be inferred. The irreversibility of Bergsonian time, said Weiner, makes possible human communication, which would have no meaning if time ran backwards. Bergsonian time acknowledges that time moves forward, that the past is irretrievable but that we might control the

⁴⁰⁰ Porter, Theodore M. "Time's Arrow and Statistical Uncertainty in Physics and Philosophy." In *The Rise of Statistical Thinking: 1820-1900*, 193-227. Princeton: Princeton University Press, 1986.

⁴⁰¹ Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*, 30-44. Cambridge, MA: The MIT Press, 1948, pp. 37-48. See also, Gibbs, Josiah Willard. *Elementary Principles in Statistical Mechanics: Developed with Special Reference to the Rational Foundation of Thermodynamics*. New York: Charles Scribner's Sons, 1902.

⁴⁰² Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, p. 93.

future to some extent by adjusting present conditions.⁴⁰³ The PDP contributor and American cognitive scientist Paul Smolensky (1955-) used a Gibbs-inspired probability distribution in his articulation of harmony theory as a paradigm for the computational development of cognitive systems which accounted for the fact that dynamical systems evolve over time.⁴⁰⁴ PDP modelers assumed, in others words, the need to construct neural models that progressively adapt; if brains could not return to former states, they reasoned, neither should neural models.

In the mid-1930s, the American mathematician, electrical engineer and cryptographer, Claude Shannon (1916-2001) realized the possibility of applying symbolic logic to create an orderly system for controlling electrical relay switches used to route calls through a complex network of telephone exchanges. He connected electricity and logic through the simple idea that electricity either passes through a relay switch or it does not; an open switch communicates the fact that electric current passes through the circuit. In framing this phenomenon as the conveyance of a message with meaning—open or closed, yes or no—Shannon spent the ensuing years creating a generalized probabilistic theory of intelligence transmission within intricately patterned structures. Specifying the physicality of his notion of information and understanding that communication entails loss of information as it routes through circuitous systems, Shannon extended the thermodynamic concept of entropy—disorder in a system—to explain the probability of information loss (i.e., a loss of order) across transmission systems. By equating information with intelligence, Shannon described intelligence as a quantitative measure of change in messages as they get transmitted through a system.⁴⁰⁵

⁴⁰³ Wiener, Norbert. "Newtonian and Bergsonian Time." In *Cybernetics: Or Control and Communication in the Animal and the Machine*, 30-44. Cambridge, MA: The MIT Press, 1948.

⁴⁰⁴ Smolensky, P. "Information Processing in Dynamical Systems: Foundations of Harmony Theory." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 1: Foundations*, 194-281. Cambridge, MA: The MIT Press, 1986.

⁴⁰⁵ Gleick, James. "Prologue" and "Information Theory." In *The Information: A History, a Theory, a Flood*, 3-12, 204-232. New York: Pantheon Books, 2011.

In the mid-1940s, Wiener collaborated with the Hungarian-American mathematician and physicist John von Neumann (1903-1957), who focused on design principles for a generalpurpose computer. Their work originated from World War II efforts to "crack the code" and attempts at using statistical mechanics to understand complex organizational systems. Their comparison of nervous systems to complex electrical machines also touched off the formal twentieth-century study of artificial intelligence. Both Wiener and von Neumann agreed on the organizational parallels between organisms and computers, but von Neumann, a reductionist and logical positivist, cared primarily about automata theory, occupying himself with abstract mathematical theorems to construct complex organizational patterns and assemblies out of simple elements. Von Neumann's models on self-reproducing automata as the basic element of life aligned more closely with the genetic informational model of German-American biophysicist Max Delbrück (1906-1981) than with neurophysiology.⁴⁰⁶

In the 1930s, a diverse group of scientists, through their endeavors to elucidate the mechanisms of genetic transfer of information, sought to engage the question Austrian-Irish physicist Erwin Schrödinger (1887-1961) addressed later in *What is Life? The Physical Aspect of the Living Cell and Mind and Matter*. In the book, Schrödinger questioned how the laws of physics—especially the second law of thermodynamics, which states that all isolated systems must approach thermodynamic equilibrium, a stability of matter or energy flow—can explain biological organization. This question directly paralleled that of Maxwell's demon, which illustrated the conundrum of how to get order out of what the laws of physics stated should lead to disorder. By deliberately diffusing disciplinary boundaries, transdisciplinary scholars comprising the Biotheoretical Gathering group in the U.K. welcomed the colonization of biology

⁴⁰⁶ Heims, Steve J. "A Mutual Interest, But..." John von Neumann and Norbert Wiener: From Mathematics to the Technologies of Life and Death, 201-229. Cambridge, MA: The MIT Press, 1980.

by physics; by asking how physics and mathematics can decode organic nature, they helped launched the field of molecular biology.⁴⁰⁷ Thus, the linking of physics and biology through the concept of information began in the interwar years, before Wiener and von Neumann carried out their joint efforts.

Despite their mutual interest in information theory, Wiener, in contrast to von Neumann and Shannon, wanted to create a science to describe natural processes, focusing on how to mathematize intelligence represented by an organism's purpose-driven behavior.⁴⁰⁸ In 1948, Bell Telephone Laboratories announced the invention of the transistor, the tiny electric semiconductor that would soon replace the vacuum tube as a more efficient electrical relay switch. That same year, both Shannon and Wiener published their theories of communication. Both demonstrated how to distinguish "signal" from "noise" (i.e., excess or irrelevant information) through statistical mechanic formulations and helped transform the concept of energy into information while redefining entropy as a measure of a system's state of confusion. In 1958, Wiener proposed that noise might be fed back into a system (acting like an external stimulus), further complicating conceptions of stimulus-response dynamics.⁴⁰⁹

Wiener revealed that a sufficiently organized ensemble of functions (like the nervous system) could predict a future message with a fair amount of certainty by applying the statistics

⁴⁰⁷ Abir-Am, Pnina Geraldine. "The Biotheoretical Gathering, Trans-Disciplinary Authority and the Incipient Legitimation of Molecular Biology in the 1930s." *History of Science*, 25;1(1987):1-70; Abir-Am, Pnina Geraldine. "Themes, Genres and Orders of Legitimation in the Consolidation of New Scientific Disciplines: Deconstructing the Historiography of Molecular Biology." *History of Science*, 23(1985):73-117; See also, Schrödinger, Erwin. *What Is Life? The Physical Aspect of the Living Cell and Mind and Matter*. Cambridge: Cambridge University Press, 1944; Kay, Lily E. *The Molecular Vision of Life: Caltech, the Rockefeller Foundation, and the Rise of the New Biology*. New York: Oxford University Press, 1993; Olby, Robert. *The Path to the Double Helix: The Discovery of DNA*. Seattle: University of Washington Press, 1974.

⁴⁰⁸ Heims, Steve J. "A Mutual Interest, But..." John von Neumann and Norbert Wiener: From Mathematics to the Technologies of Life and Death, 201-229. Cambridge, MA: The MIT Press, 1980.

⁴⁰⁹ Satō, Shunsuke. "Role and Use of Noise in Biological Systems." In *Competition and Cooperation in Neural Nets: Proceedings of the U.S.-Japan Joint Seminar held at Kyoto, Japan, February 15-19, 1982.* Edited by S. Amari and M.A. Arbib, 111-120. New York: Springer-Verlag, 1982. See also, Wiener, Norbert. *Nonlinear Problems in Random Theory.* Cambridge, MA: The MIT Press, 1958.

of a time series and incorporating received information from the past. He believed his theory to apply to the question of Maxwell's demon which hypothetically changes the entropy of a system gradually, not instantaneously.⁴¹⁰ Wiener thus concluded that animals and machines need a stable structure to enable learning and adaptation over time. Brain theorists following Wiener correspondingly sought to incorporate neurophysiological evidence tying structure to function into their models.

Incorporating neurophysiological evidence into neural models

Emanating from the cybernetic endeavor to mathematically model processes of communication and control, brain theory approaches paralleled artificial intelligence approaches to model intelligence at midcentury and beyond. Brain theorists, taking for granted the electrically conductive model of nervous system functionality, attempted to incorporate neurophysiological evidence into neural models, but retained the original cybernetic and information theory reliance on statistical methods to construct their models. The American neurophysiologist Warren McCulloch (1898-1969) recognized the historical foundations of experimental epistemology, stating that "physiology has, from its beginning, been largely a hypothetical and deductive system in terms of postulated recognizables constructed to explain the causal relations of perceived events."⁴¹¹ Brain theory moved beyond the limits of electrophysiological experimentation, incorporating incomplete evidence from neurophysiology into neural models, turning uncertainty into probabilistic prediction.

⁴¹⁰ Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, pp. 57-69; Shannon, Claude. "A Mathematical Theory of Communication." *Bell System Technical Journal*, 27;3(1948):379-423. See also, Shannon, Claude, and Warren Weaver. *The Mathematical Theory of Communication*. Urbana: The University of Illinois Press, 1949.

⁴¹¹ McCulloch, Warren S. "A Historical Introduction to the Postulational Foundations of Experimental Epistemology." In *Embodiments of Mind*, 359-372. Cambridge, MA: The MIT Press, 1965, p. 359.

In 1943, McCulloch and the American mathematician Walter Pitts (1923-1969), two members of the Macy conferences cybernetics group whose work featured prominently in Wiener's *Cybernetics*, attempted to devise a way to deduce what psychologists called "mental activities" from neurophysiology. They adhered to the binary all-or-none principle in their project of experimental epistemology by building the first mathematical model which attempted to describe "neural events and the relations among them."⁴¹² The all-or-none principle—that neurons effectively transmit electrical messages or they do not—posited a binariness to nervous communication and was fundamental to early mathematical models of neuronal activity.⁴¹³

McCulloch, who wanted to use a science of signals and messages as a bridge between physiology and psychology, spent a career seeking mechanisms to describe cognitive functions and asking how the logical structure of the mind related to neurophysiology and madness. In the 1930s he conducted research stimulating the cortex of monkeys to map out its functional pathways with the Dutch neurophysiologist Johannes Dusser de Barenne (1885-1940). Much of this work involved mapping out the functional topographic boundaries of the sensorimotor cortex. With a background in neurophysiology and some understanding of the functional organization of the nervous system, McCulloch set out on a project of organic reductionism,

⁴¹² McCulloch, Warren S., and Walter Pitts. "A Logical Calculus of the Ideas Immanent in Nervous Activity." *Bulletin of Mathematical Biophysics*, 5(1943):115-133, p. 115. See also, McCulloch, Warren S. *Embodiments of Mind*. Cambridge, MA: The MIT Press, 1965; Kay, Lily E. "From Logical Neurons to Poetic Embodiments of Mind: Warren S. McCulloch's Project in Neuroscience." *Science in Context*, 14;4(2001):591-614; Abraham, Tara H. "(Physio)logical Circuits: The Intellectual Origins of the McCulloch-Pitts Neural Networks." *Journal of the History of the Behavioral Sciences*, 80;1(2002):3-25.

⁴¹³ Adrian's work with British physiologist Keith Lucas led to their formulation of the all-or-none principle. See Adrian, Edgar D. "The All-or-None Principle in Nerve." *The Journal of Physiology*, 47;6(1914):460-474; Lucas, Keith. "Croonian Lecture: The Process of Excitation in Nerve and Muscle." *Proceedings of the Royal Society of London B*, 85;582(1912):495-524.

seeking a material basis to Kant and Leibniz's ideas about the representation of knowledge and a corresponding desire to overcome Cartesian dualism.⁴¹⁴

In considering the nervous system as a series of nets of neurons, McCulloch and Pitts drew from the logical positivist Rudolf Carnap (1891-1970) and the mathematical and propositional logic of Bertrand Russell and Alfred North Whitehead to develop a formal theory of language which could describe how the nervous system produces mental activities. They claimed their theory could "calculate the behavior of any net."⁴¹⁵ The authors incorporated the concept of neuronal inhibition as a feedback mechanism of control as central to their model. They also included Spanish neuroanatomist and neurophysiologist Rafael Lorente de Nó's reverberating circuits theory as an explanatory mechanism of continuous, regenerative activity.⁴¹⁶ While accounting for synaptic delay in neuronal transmission (i.e., non-instantaneous processing), the McCulloch-Pitts model looped nervous impulses in circles endlessly, patterning the message as an "eternal idea," a memory which existed as long as reverberation endured.⁴¹⁷ Like Shannon's information theory and Wiener's cybernetics, the McCulloch-Pitts model revealed through propositional logic the considerable modifications in system operations that can occur if modelers of communication and control look at systems from the point of view of process instead of at final states. McCulloch also claimed that their regenerative loop model

⁴¹⁴ Heims, Steve J. "Describing 'Embodiments of Mind': McCulloch and his Cohorts." In *The Cybernetics Group: Constructing a Social Science for Post-War America*, 31-51. Cambridge, MA: The MIT Press, 1991; Dusser de Barenne, J. G., and Warren S. McCulloch. "Functional Boundaries in the Sensori-Motor Cortex of the Monkey." *Proceedings of the Society for Experimental Biology and Medicine*, 35;2(1936):329-331. For more on McCulloch, see Abraham, Tara H. *Rebel Genius: Warren McCulloch's Transdisciplinary Life in Science*. Cambridge, MA: The MIT Press, 2016.

⁴¹⁵ McCulloch, Warren S., and Walter Pitts. "A Logical Calculus of the Ideas Immanent in Nervous Activity." *Bulletin of Mathematical Biophysics*, 5(1943):115-133, p. 119.

 ⁴¹⁶ McCulloch, Warren S., and Walter Pitts. "A Logical Calculus of the Ideas Immanent in Nervous Activity."
 Bulletin of Mathematical Biophysics, 5(1943):115-133. See also, Kay, Lily E. "From Logical Neurons to Poetic Embodiments of Mind: Warren S. McCulloch's Project in Neuroscience." *Science in* Context, 14;4(2001):591-614.
 ⁴¹⁷ McCulloch, Warren S. "Why the Mind is in the Head." In *Embodiments of Mind*, 72-87. Cambridge, MA: The MIT Press, 1965, p. 77.

proved, thanks to the Austro-Hungarian mathematician and analytic philosopher Kurt Gödel's (1906-1978) arithmetization of intuitionistic symbolic logic, that all general Turing machines man-made or organic—could deductively compute any computable number given a properly constructed net.⁴¹⁸

At the 1950 Macy cybernetics meeting, recent neurophysiological findings engaged attendees.⁴¹⁹ The possibility that individual neurons might code not just digitally, but also in analog challenged Forbes' assertion that nerve fibers transmit messages "without modification."⁴²⁰ During the American neurophysiologist Ralph Gerard's presentation on the subject, Wiener remarked that processes like learning are likely not purely digital, and believed analog computing important to the future construction of machines:

I think that the freedom of constructing machines which are in part digital and in part analogical is a freedom which I profoundly believe to exist in the nervous system, and it represents, on the other hand, with humanly made machines, possibilities which we should take advantage of in the construction of the automaton.⁴²¹

Gerard went on to speculate that the discrete firing of action potentials might not be what carries the informational content in messages, it could instead be something to do with the total accumulation of impulses at particular times and places in the nervous system. He posited that perhaps by paying attention to the physiological "forbidden continuous region," that is, departing

⁴¹⁸ McCulloch, Warren S. "What is a Number, that a Man May Know It, and a Man, that he May Know a Number?" in *General Semantic Bulletin*, 26-7(1960):7-18.

⁴¹⁹ This was the seventh of ten annual Macy Conferences on cybernetics. The conference series was titled *Cybernetics: Circular Causal and Feedback Mechanisms in Biological and Social Systems*. The Macy Conferences aimed to promote interdisciplinary communication and collaboration on specific scientific topics.

⁴²⁰ Forbes, Alexander. "The Interpretation of Spinal Reflexes in Terms of Present Knowledge of Nerve Conduction." *Physiological Reviews*, 2;3(1922):361-414, p. 361.

⁴²¹ Foerster, Heinz von (ed.). *Cybernetics: Transactions of the Seventh Conference, March 23-24,* 1950. New York: Josiah Macy, Jr. Foundation, 1951, p. 18.

from the all-or-nothing concept of nervous transmission, scientists might uncover the "critical mechanism" in nervous system functioning by considering, for example, whether subthreshold responses (i.e., electrical changes in a neuron which do not result in an action potential) play a role in transmission.⁴²² Bigelow noted a potential point of incommensurability between physiologists and "most people who are approaching this Conference from a mathematical or machine side, as I do," in stating:

What we mean by neurons are not cells as they are described in somebody's book on cell structure; we mean that the neural cell is exactly that part of the system which has the property of carrying out processes of like computation, that is, the property of carrying out operations which are in fact digital.⁴²³

Despite Bigelow's apparent dismissiveness and adherence to the notion of a neuron as an abstract entity, an analogical aid in cybernetic reasoning, a 1952 paper by the British physicist Donald MacKay (1922-1987) and McCulloch shows logicians did think about adapting their neural models. In the paper the pair considered "how efficiently a typical neuronal link, or 'synapse,' could be used to convey information" beyond the temporal limitations imposed by the binary all-or-none model used in the 1943 McCulloch and Pitts paper.⁴²⁴ Neurophysiological research showing summation of activity over time as well as direct monosynaptic inhibition and excitation in reflex arcs helped Pitts and McCulloch formulate their 1947 vector-matrix model for how neural mechanisms perceive auditory and visual forms. The architecture of the model

⁴²² Foerster, Heinz von (ed.). *Cybernetics: Transactions of the Seventh Conference, March 23-24, 1950.* New York: Josiah Macy, Jr. Foundation, 1951, pp. 45-46.

⁴²³ Foerster, Heinz von (ed.). *Cybernetics: Transactions of the Seventh Conference, March 23-24, 1950.* New York: Josiah Macy, Jr. Foundation, 1951, p. 47.

⁴²⁴ MacKay, Donald M., and Warren S. McCulloch. "The Limiting Information Capacity of a Neuronal Link." *The Bulletin of Mathematical Biophysics*, 14;2(1952):127-135, p. 128.

represented repeated patterns of neural connections in the cortex. In attempting to properly map sets of logical operators to nets of neurons, Pitts and McCulloch acknowledged an inherent structural and functional organization of the nervous system which was obviously important for perception and which should be reflected in neural model architectures, but preferred the conception of activity distribution among networks of neurons over the Gestalt psychology-inspired insistence of physical traces or mosaics as materially representing the localized information necessary for recognition of forms. The pair also accounted for the known anatomical pattern of neuronal projections to the mammalian visual cortex from the lateral geniculate of the thalamus and to the superior colliculus revealed through previous research.⁴²⁵

Von Neumann's 1958 book, *The Computer and the Brain*, expanded on his general interest in the analogies between computers and brains and reasoned that nervous systems, which have slower physical components of communication but more complex connections compared to computers, probably carry out their operations in parallel, while computers process information in sequence.⁴²⁶ An influential 1959 paper co-authored by McCulloch with Pitts and the American electrical bioengineer and communications physiologist (and future cognitive scientist) Jerome Lettvin (1920-2011) and Chilean biologist (and future philosopher) Humberto Maturana (1929-), provided neurophysiological evidence supporting von Neumann's claims. The four scientists demonstrated through electrophysiological experimentation that electrical impulses emanating from a frog's retina transmit "in a language already highly organized and interpreted" through to

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⁴²⁵ Pitts and McCulloch for the first time mathematically represented interconnected inputs and outputs with a vector-matrix approach. Pitts, Walter, and Warren S. McCulloch. "How We Know Universals: The Perception of Auditory and Visual Forms." *Bulletin of Mathematical Biophysics*, 9(1947):127-147; Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948, pp. 22-23, 139-143; Heims, Steve J. "Gestalten Go to Bits, 2: Köhler's Visit." In *The Cybernetics Group: Constructing a Social Science for Post-War America*, 224-247. Cambridge, MA: The MIT Press, 1991.
⁴²⁶ Originally delivered as the Silliman Lectures at Yale in 1956. Von Neumann, John. *The Computer and the Brain*. New Haven: Yale University Press, 1958.

the central nervous system in a topographic arrangement via the optic nerve bundle to the superior colliculus. They described the retinal output in terms of four operations projecting to four corresponding and "parallel sheets of endings" in the frog's brain which detect different aspects of a visual stimulus and depend on the general illumination of an object. The four distinct patterns detected by the four distinct types of nerve fibers in the retina were: edges and contrast, curvature of edges, movement of edges, and dimming produced by movement or rapid darkening. Their work provided crucial evidence for the organized transmission of information as arranged and distributed across the retina.⁴²⁷

In 1960, the English psychiatrist and cybernetician W. Ross Ashby (1903-1972), who attended many of the Macy cybernetics conferences, significantly revised his 1952 *Design for a Brain: The Origin of Adaptive Behavior* based on improved "understanding of brain-like mechanisms."⁴²⁸ Compared with McCulloch's experimental epistemology, Pickering described Ashby's conception of how the brain produces adaptive behavior as an experimental ontology. Drawing from Lorente de Nó and McCulloch and Pitt's ideas about interconnected nets of neurons, Ashby described narratively as well as mathematically how the brain's many sets of interconnected nets of neurons act semi-independently as adaptive homeostats trying to achieve equilibrium in reaction to changes from incoming stimuli. A fully interconnected network would take too long to reach equilibrium, calculated Ashby, but a sparsely interconnected network in which semi-autonomous units (i.e., nets of neurons) arrive at equilibrium sequentially made temporal sense. Our brain is sparely interconnected, said Ashby, because the world is, too; the world consists of many environmental variables which are only sparsely interconnected with one

⁴²⁷ Lettvin, J. Y. et al. "What the Frog's Eye Tells the Frog's Brain." *Proceedings of the IRE*, 47;11(1959):1940-1959, p. 1950.

⁴²⁸ Ashby, W. Ross. *Design for a Brain: The Origin of Adaptive Behavior*. New York: John Wiley & Sons, 1960, p. vii.

another.⁴²⁹ Ashby's analysis of the brain as a complex system removed the thermodynamic constraint which imposed a fixed quantity of energy within complex systems; by imagining a free supply of energy, control between nets of neurons—independent subsystems—could flow in any direction.⁴³⁰

In his 1972 The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory, Michael Arbib (1940-), the English-born theoretical neuroscientist and computer scientist who was advised by Wiener and spent his career at U.S. academic institutions, argued that the cybernetic metaphor of "humans are machines" should not be used to reduce humans to machines, but as a way to use machines to learn about brains, and vice versa.⁴³¹ Arbib claimed that the four major texts which shaped cybernetics and theoretical neurophysiology up to that point were Wiener's Cybernetics (1948), Hebb's The Organization of Behavior (1949), Ashby's Design for a Brain (1960) and the papers collected in McCulloch's *Embodiments of Mind* (1965). According to Arbib, the appropriate cybernetic approach to modeling the functional processes of the nervous system required that the internal structure of any neural model be similar to the real organizational structure of nervous systems. Arbib thus distinguished between artificial intelligence and brain theory approaches. Proper brain theory, for example, must account for the neurophysiological evidence pointing to the distributed control of movement by the nervous system, which requires integration of information within and across brain regions.

⁴²⁹ Pickering, Andrew. "Ross Ashby: Psychiatry, Synthetic Brains, and Cybernetics." In *The Cybernetic Brain: Sketches of Another Future*, 91-170. Chicago: The University of Chicago Press, 2010.

 ⁴³⁰ Ashby, W. Ross. *Design for a Brain: The Origin of Adaptive Behavior*. New York: John Wiley & Sons, 1960.
 ⁴³¹ Arbib began to lay out the thrust of this argument a decade prior to the publication of *The Metaphorical Brain*. See Arbib, Michael. *Brains, Machines, and Mathematics*. New York: McGraw Hill, 1964.

The Metaphorical Brain, therefore, laid out specific organizational principles for designing a brain mathematically. Focusing on perception over behavior and careful not to make the mistake of "radical behaviorism that confuses thought with action," Arbib wanted to construct a neural model that stressed "action-oriented perception" which posited that the purpose of the nervous system's ability to perceive and recognize objects was not to classify them, but to interact with them.⁴³² A modified Pitts and McCulloch feedback tracking scheme was integral, as was McCulloch's "principle of redundancy of potential command" which stated that the power to control integrated neural activity by any particular net or region should depend on where the most relevant information resides.⁴³³ The possibility of changing locus of control presumed that the brain processes information parallelly in a highly distributed fashion, and therefore is not under the centralized control of any single executive region. The key concept that brain theory shared with cybernetics is that of *change as information*. Lashley's work from four decades prior showing that impairments of rat maze-running behavior depended on removing the amount of cortex, not necessarily which part, supported Arbib's contention that many parts of the brain might contribute equally to problem-solving and that brain computation involves "the cooperation of many subroutines that are working simultaneously in parallel."434

Emerging neurophysiological evidence provided brain theorists with functional and anatomical attributes that helped in model construction. Based on experimental findings

⁴³² Arbib, Michael. *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory*. New York: Wiley Interscience, 1972, p. 16.

⁴³³ McCulloch cited the example of a naval fleet to support his claim: whichever individual ship that first receives an enemy signal helps control the behavior of the whole fleet. In other words, the point of control of the brain does not have to depend on any one region. In a naval fleet at war, therefore, each ship acts as "a quasi-automaton, with its own multiple closed loop servosystems of information, like the segments of the caudata" (a brain region). McCulloch, Warren S. "Where is Fancy Bred?" In *Embodiments of Mind*, 216-229. Cambridge, MA: The MIT Press, 1965, p. 226.

⁴³⁴ Arbib, Michael. *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory*. New York: Wiley Interscience, 1972, p. 169.

regarding "the visual world of an animal," Arbib declared that the "most crucial information is contained in change—change in space and change in time."⁴³⁵ Moving spot detector neurons found in the retinas of frogs and cats performed "preprocessing" of temporal changes occurring in the visual field.⁴³⁶ Experimenters discovered spatial change detectors in the cortex of mammals as well. Beginning in 1959, the Canadian American neurophysiologist David Hubel (1926-2013) and Swedish neurophysiologist Torsten Wiesel (1924-), who would later share the Nobel Prize for their work, carried out experiments recording electrical impulses from neurons in the visual cortex of cats and monkeys as they perceived visual objects in their field of view. The pair's findings described neurons' receptive fields as mechanistic functions of visual input—"simple" cortical cells in the primary visual cortex (the first cortical area receiving neuronal projections from the midbrain) responded to lines (the visual stimulus) of specific orientations in specific places in the visual field; "hypercomplex" cells in other areas of the visual cortex responded to angles of specific sizes and orientations across locations in the visual field.⁴³⁷

In order to make sense of objects in the visual world, reasoned Arbib, the nervous system must somehow integrate the distributed and local information processed by semi-autonomous populations of neurons. Research revealing somatotopically-organized arrangements in the sensorimotor and visual systems, for example, supported this idea. Arbib also said that depending on the particular function of a neural network, it might encode information differently

⁴³⁵ Arbib, Michael. *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory*. New York: Wiley Interscience, 1972, p. 51.

⁴³⁶ Arbib, Michael. "Action-Coding and Neural Networks." *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory*, 14-54. New York: Wiley Interscience, 1972.

⁴³⁷ Hubel, D. H., and T. N. Wiesel. "Receptive Fields, Binocular Interaction and Functional Architecture in the Cat's Visual Cortex." *The Journal of Physiology*, 160;1(1962):106-154; Hubel, D. H., and T. N. Wiesel. "Receptive Fields and Functional Architecture in Two Nonstriate Visual Areas (18 and 19) of the Cat." *Journal of Neurophysiology*, 28;2(1965):229-289; Hubel, D. H., and T. N. Wiesel. "Receptive Fields and Functional Architecture of Monkey Striate Cortex." *The Journal of Physiology*, 195;1(1968):215-243; See also, Hubel, D. H., and T. N. Wiesel. *Brain and Visual Perception: The Story of a 25-Year Collaboration*. New York: Oxford University Press, 2005.

from other networks. Thus, Arbib's perceptual brain theory reliance on "action-oriented coding" favored neurophysiological research which sought to understand which specific aspects of a stimulus or behavior can be represented by the activity of neurons.⁴³⁸ This paradigm stemmed from original information theory and cybernetic theory ideas, later forming the basis of artificial intelligence studies, in which neurons act as symbolic processing units that signal a particular meaning about the stimulus.

Nervous information processing as microstructural change

While Arbib's articulation of brain theory acknowledged the neurophysiological evidentiary support that the brain processes information in parallel, not in sequence (as computers did), he admitted that the limitations of testing the theory with computing machines meant he had to translate the parallel algorithm into a serial one.⁴³⁹ Artificial intelligence research from the 1960s through 1980s relied primarily on rule-based symbolic processing. The linguistic theory of the American philosopher Noam Chomsky (1928-) similarly assumed the process of language learning relied on explicit rule formation made possible through logical structures.⁴⁴⁰ In the 1980s, a group of researchers gathered to promote an alternative neurally-inspired approach to modeling cognition called parallel distributed processing, reviving a modeling paradigm which had laid fallow for nearly two decades—connectionism.⁴⁴¹

⁴⁴¹ For a personal account of artificial intelligence and deep learning research beginning from the 1960s see Sejnowski, Terrence J. *The Deep Learning Revolution*. Cambridge, MA: The MIT Press, 2018. See also, McLaughlin, Brian P. "The Connectionism/Classicism Battle to Win Souls." *Philosophical Studies: An*

International Journal for Philosophy in the Analytic Tradition, 71;2(1993):163-190; Schneider, Walter.

"Connectionism: Is it a Paradigm Shift for Psychology?" *Behavior Research Methods, Instruments & Computers.* 19;2(1987):73-83.

⁴³⁸ Arbib, Michael. *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory*. New York: Wiley Interscience, 1972, pp. 14-30.

⁴³⁹ Arbib, Michael. *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory*. New York: Wiley Interscience, 1972, pp. 71-72.

⁴⁴⁰ See Chomsky, Noam. *The Logical Structure of Linguistic Theory*. New York: Springer, 1975.

In 1957, the American psychologist and neurobiologist Frank Rosenblatt (1928-1971) built the perceptron—the first learning machine—based on punishment and reinforcement learning principles from behaviorism. Shaped by concepts like Hebb's cell-assembly and the Pitts-McCulloch model of neural connection patterns, the perceptron model represented an early attempt at neural network connectionism-inspired modeling.⁴⁴² By the end of the 1960s, however, the limitations of perceptron models in pattern recognition, knowledge representation and learning tamped down researcher interest in connectionism. The 1969 book *Perceptrons* by American cognitive scientists Marvin Minsky (1927-2016) and Seymour Papert (1928-2016; who was South African-born), detailed an inability of perceptrons to recognize certain patterns as having to do with the schematic architecture of computational models of parallelism. The fallout from *Perceptrons* led to widespread abandonment of connectionist approaches to modeling intelligence.⁴⁴³

In the 1980s, cognitive science researchers resuscitated connectionist theories based on parallel information processing. In 1986, the American cognitive psychologists David Rumelhart (1942-2011), James McClelland (1948-), and the PDP (parallel distributed processing) research group published their two-volume *Parallel Distributed Processing: Explorations in the Microstructure of Cognition* as an attempt to construct neurally-inspired models of information processing centered on the assumption the nervous system computes in parallel (not sequentially), an assertation von Neumann made in 1958. The PDP research group, ranging from five to 15 or more psychologists, cognitive scientists, computer scientists, biologists, and

⁴⁴² Rosenblatt, F. "The Perceptron: A Probabilistic Model for Information Storage and Organization in the Brain." *Psychological Review*, 65;6(1958):386-408.

⁴⁴³ See Minsky, M. and S. Papert. *Perceptrons: An Introduction to Computational Geometry*, Expanded Edition. Cambridge, MA: The MIT Press, 1988, pp. vii-xv, 1-20. This book, together with the 1973 Lighthill report which was critical of artificial intelligence (AI) research, led to drastic AI funding cuts in the U.K. and U.S. This was later referred to as the beginning of the first AI winter.

linguists, met regularly at the University of California, San Diego (UCSD) beginning in 1981, though Rumelhart and McClelland's interest in distributed and associative memories arose from conversations with the American psychologist and neuroscientist Jim Anderson (1940-) beginning in 1968 and ramped up considerably as they developed an interactive activation model of word perception in 1979, when the English-Canadian psychologist and computer scientist Geoffrey Hinton (1947-) was a postdoctoral fellow at UCSD.⁴⁴⁴

The PDP approach rested on several assumptions about human cognition, but ultimately took for granted that the brain is in a constant process of changing and improving in order to become its optimized self. The first assumption was that cognitive processes—perception, memory, language, and higher-level thought processes—are distributed and constructed in and by the nervous system. Memory, for example, does not reside in locally-represented physical traces, as Gestalt psychology and symbolic processing systems assumed. Memory is distributed, rather, across the activity of varied and interconnected neural networks.

The PDP approach also assumed that connections between neurons change during processing. Shaped by the Hebb rule concept of pattern association—that synaptic activation leads to a strengthening of connections between neurons—the PDP research group presented models composed of individual processing units which could interact with and constrain each other by sending excitatory and inhibitory signals. A specific item presented to the visual field, for example, would trigger a specific sequential pattern of activation, exciting (or inhibiting) processing units along the processing stream while also strengthening (or weakening) connections between processing units by small adjustments so as to facilitate subsequent

⁴⁴⁴ McClelland, James L., and David E. Rumelhart. "Preface." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition: Foundations, Volume 1*, ix-xiii. Cambridge, MA: The MIT Press, 1986. The PDP research group included Francis Crick, co-proposer of the double helix structure of DNA (see "Acknowledgements," p. xi).

processing.⁴⁴⁵ The ability of the nervous system to compute in analog and not exclusively in digital (i.e., encoding continuous data as opposed to discrete chunks), alluded to by Gerard in his 1950 presentation to the cybernetics group, found a home in PDP strategies as connection strength adjustments. PDP also fixed the closed paths problem of McCulloch-Pitts model. Their reverberatory circuits were closed paths, but the individual processing units of PDP models were fluidly connected and able to change based on changing activation patterns.

The crucial difference between PDP models and other models of cognitive processes up to that point was their definition of cognition as represented in the brain. Models before PDP stored knowledge as a static copy of a pattern of connections between units. In PDP models, on the other hand, the patterns themselves were not stored (as data on a real computer hard drive, but also metaphorically in the brain); what was stored were the connection strengths between units that allowed patterns of activation to be re-created. Put another way, the knowledge about any individual pattern was not stored in the connections of a special unit reserved for that pattern, but was distributed over the connections over a large number of processing units. In the old system, the information being processed was distinguished from the structure itself. In the PDP system, the structure *was* the information; the process of making structural adjustments through connection modulation *was* the process of learning. In PDP, the basis of all cognitive nervous system functioning is a learning mechanism at the microstructural level.

Whereas previous connectionism-inspired neural models continued with symbolic processing strategies, PDP-type connectionism abolished the need for model builders to attempt

⁴⁴⁵ McClelland, James L., Rumelhart, David E., and G. Hinton. "The Appeal of Parallel Distributed Processing." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition: Foundations, Volume 1*, 3-44. Cambridge, MA: The MIT Press, 1986; McClelland, James L. "Memory as a Constructive Process: The Parallel Distributed Processing Approach." In *The Memory Process: Neuroscientific and Humanistic Perspectives*. Edited by S. Nalbantian, P. M. Matthews, and James L. McClelland, 129-155. Cambridge, MA: The MIT Press, 2011.

to reconstruct the underlying structure of nervous system processing. Taken together, PDP theories amounted to a dramatic reconceptualization of how the nervous system processes information and represents knowledge, yet they centered on the conception of cognition as reduced to nervous system functionality rooted in the movement of electric current. In the eighteenth century, in attempting to explain how our internal intuition engaged in discourse with an external object, Kant raised the problem of how to identify schemata, or rules for interpreting general and abstract concepts into particular spatiotemporal forms and sensory images. The conundrum persisted among twentieth-century scientists who assumed we must know something about the schemata, scripts, or frames the nervous systems uses to process information in order to build appropriate neural models.⁴⁴⁶ The PDP approach rendered the point moot by conceiving of knowledge as equivalent to schemata. According to the PDP research group, cognition emerges from the interaction of the brain's microstructure—a multitude of individual processing units that self-modulate their connection strengths.

Generally, a PDP system changed connection strengths between processing units as an attempt to get back to a state of stable equilibrium, but PDP allowed for various learning strategies for the system to adjust connection strengths. Some used Shannon's formulation of uncertainty as a way to instruct the model to alter connection strengths depending on missing information in the system's probability distributions.⁴⁴⁷ Others used adapted Hopfield nets,

⁴⁴⁶ Hanna, Robert. "Kant's Theory of Judgment." In *The Stanford Encyclopedia of Philosophy*. Winter 2018 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/entries/kant-judgment/index.html; Hanna, Robert.
"Completing the Picture of Kant's Metaphysics of Judgment." In *The Stanford Encyclopedia of Philosophy*. Winter 2018 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/entries/kant-judgment/supplement5.html; Rumelhart, David E., Smolensky, P., McClelland, James L., and G. E. Hinton. "Schemata and Sequential Thought Processes in PDP Models." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 2: Psychological and Biological Models*, 7-57. Cambridge, MA: The MIT Press, 1986. See also, Minsky, M. "Steps Toward Artificial Intelligence." *Proceedings of the IRE*, 49;1(1961):8-30.

⁴⁴⁷ Smolensky, P. "Information Processing in Dynamical Systems: Foundations of Harmony Theory." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 1: Foundations*, 194-281. Cambridge, MA: The MIT Press, 1986.

recurrent neural networks that find energy minima as a way to encode information in a system using the thermodynamic principles of statistical mechanics.⁴⁴⁸ Other models used the learning strategy of backpropagation to allow information to flow backward through a multi-layered neural network, helping it to assess and adjust connection values.⁴⁴⁹

PDP attempts to "physiologize" the neural models of intelligence were an outgrowth of the original McCulloch-Pitts project of mapping physiological variables onto corresponding sets of logic operators. Neurophysiological evidence pointing to the distribution of memory throughout the nervous system mounted in the decades between McCulloch, Pitts and PDP. The famous case of H.M., who exhibited retrograde amnesia upon bilateral removal of the hippocampus in the midbrain, however, presented difficulties for distributed memory models. A PDP model reconciled the problem by assuming the brain stores recent memories separately from older ones.⁴⁵⁰

PDP, which posited learning as naturally resulting from the operation of the system, offered a new way to think about information processing by the nervous system. The symbolic processing approach emphasized understanding the meaning between an object or stimulus and the corresponding interpretation by the nervous system. The PDP approach, in contrast, placed meaning in the changing nervous system itself; it helped redefine cognitive functioning as an

⁴⁴⁸ Hinton, G. E., and T. J. Sejnowski. "Learning and Relearning in Boltzmann Machines." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 1: Foundations*, 283-317. Cambridge, MA: The MIT Press, 1986. See also, Hopfield, J. J. "Neural Networks and Physical Systems with Emergent Collective Computational Abilities." *Proceedings of the National Academy of Sciences of the United States of America*, 79(1982):2554-2558.

⁴⁴⁹ Rumelhart, David E., Hinton, G. E., and R. J. Williams. "Learning Internal Representations by Error Propagation." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 1: Foundations*, 318-362. Cambridge, MA: The MIT Press, 1986.

⁴⁵⁰ McClelland, James L., and David E. Rumelhart. "Amnesia and Distributed Memory." In *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 2: Psychological and Biological Models*, 503-527. Cambridge, MA: The MIT Press, 1986. See also, Scoville, William Beecher, and Brenda Milner. "Loss of Recent Memory after Bilateral Hippocampal Lesions." *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1957):11-21.

emergent property of microstructural learning mechanisms. Put simply, it equated human cognition with an ability to learn and adapt.

Conclusion

The mechanistic fact that neural processes transpire through the movement of electric current framed notions of neurophysiological function and cognition which were embedded in cybernetic brain theories and neural models through the late twentieth century. According to this functional framework, it is the nature of the nervous system to be electrically active. Humans adapt through the action of their electrified brains, turning uncertainty into sureness. More than this, activity *is* adaptation, as the PDP approach makes explicit. Neurophysiological experiments and theories from the mid-nineteenth century onward have reified the notion of adaptive (re)construction as essential to human nature. The Hegelian concept of becoming is now folded into the very definition of how a brain functions at a fundamental mechanistic level—it is constantly progressing to new optimums, shifting the goalposts of equilibrium via electrical currents and changing synaptic connections.

The impact of World War I facilitated movements of disillusionment and disenchantment with the world which impacted cultural and epistemological shifts within science.⁴⁵¹ After World War II, psychologists and social scientists combined efforts to achieve a common purpose, aiming to rebuild the world according to a worldview. The guiding principle of humanistic psychologists was self-actualization; we could improve the world, they said, through selfimprovement.⁴⁵² Cybernetics, shaped by the positivist tradition, appealed to social scientists who

⁴⁵¹ Forman, Paul. "Weimar Culture, Causality, and Quantum Theory, 1918-1927: Adaptation by German Physicists and Mathematicians to a Hostile Intellectual Environment." *Historical Studies in the Physical Sciences*, 3(1971):1-115.

⁴⁵² See e.g., Grogan, Jessica. *Encountering America: Humanistic Psychology, Sixties Culture & the Shaping of the Modern Self.* New York: Harper Perennial, 2013.

were interested in systems of communication and control as means to understand interpersonal and intergroup behavior. Their ultimate goal was to create a scientific sociology which understood how to properly structure and manage a democratic society and prevent the spread of communism.⁴⁵³

Wiener, skeptical of the feasibility of a science of social management, thought sociologists had to follow from physicists by embracing statistical methods that could account for random phenomenon. Likening social organization to neural organization as well-structured in some aspects but haphazard in others, Wiener, citing Ashby's work outlined in *Design for a Brain*, reasoned that a stable system should have only the minimum amount of structured connection so that it could learn. In other words, stable systems by definition have some instability built-in. For Wiener this idea shed light on the question of the appropriate amount of centralization vs. decentralization in government; governments need some input from small, local and de-regulated organizations in order to be adaptable to change. Thinking about knowledge and learning "in terms of process rather than accomplishment," said Wiener, suggests that "governmental organisation is subject to an analysis from the point of view of control theory and that this analysis may in time become a valid guide for practical organisations."⁴⁵⁴

Wiener's cybernetics arose from a World War II necessity of knowing the enemy's actions. In the context of othering the enemy, cybernetics helped forge an "identity of intention and self-correction" and an understanding of ourselves through the boundary between us and the

⁴⁵³ Heims, Steve J. "Midcentury, U.S.A." In *The Cybernetics Group: Constructing a Social Science for Post-War America*, 1-13. Cambridge, MA: The MIT Press, 1991. See also, Turner, Fred. "Therapeutic Nationalism." In *The Democratic Surround: Multimedia and American Liberalism from World War II to the Psychedelic Sixties*, 213-258. Chicago: The University of Chicago Press, 2013.

⁴⁵⁴ Typescript of "Some Physical Analogies in Sociology," 1950, Box 29B, Folder 661, Norbert Wiener papers, MIT Distinctive Collections, Cambridge, MA, USA, pp. 13-14. For more on Wiener's skepticism, see also, Heims, Steve J. *The Cybernetics Group: Constructing a Social Science for Post-War America*. Cambridge, MA: The MIT Press, 1991, p. 28.

enemy. Wiener's cybernetics thus reflected a world in which "the individual lived in isolation, struggling (searching for tactics) to create order out of chaos."⁴⁵⁵

Wiener helped reframe biological determinism as probability through an invocation of thermodynamic principles and statistical methods for theories of communication and control. Brain theorists and their neural models used statistics to turn uncertainty into knowledge through a taken-for-granted framework of nervous system functionality underwritten in the movement of electric current. Electric current, the implicit peddler of nervous system information processing, is transmitted within a body, but not between them.

Theories of nervous information processing through the 1980s (where, as does the Cold War, this investigation ends) relied on the well-established use of probabilistic mathematics in the sciences which was brought to bear on organic life through cybernetic theories of communication and control originating in the 1940s. Neurologically-inspired models of cognition also must be understood as emanating from the wartime imperative to "crack the code" as well as in the twentieth-century context of changing discourse about the meaning of a healthy body and the individual responsibility to maintain one, though their connections are not the focus of this work.⁴⁵⁶ Relatedly, neural models of cognition, underwritten by the electrical conductive model of nervous system processing, also must be understood as in conversation with the psychological disciplines which have profoundly shaped the types of persons we are able to be, opening up diverse ways to inspect, problematize, evaluate, disclose, cure, and give significance

⁴⁵⁵ Galison, Peter. "The Ontology of the Enemy: Norbert Wiener and the Cybernetic Vision." *Critical Inquiry*, 21;1(1994):228-266, pp. 263, 266.

⁴⁵⁶ See e.g., Porter, Dorothy. *Health Citizenship: Essays in Social Medicine and Biomedical Politics*. Berkeley: University of California Medical Humanities Press, 2011. See also, Rose, Nikolas. *The Politics of Life Itself: Biomedicine, Power, and Subjectivity in the 21st Century*. Princeton: Princeton University Press, 2006.

to the self.⁴⁵⁷ Cybernetic discourse also led to significant scholarship considering the social and cognitive implications of changing human-machine relations.⁴⁵⁸ Yet, because they are fundamentally underwritten by a mathematical modeling analytical framework embraced first by their cybernetician predecessors, computational neural models that emerged in the second half of the twentieth century represented a new form of mechanism in which their implicit espousal of a Hegelian model of incessant becoming was undermined by a mechanistic philosophy. Despite a new framing and representation of the self, PDP models presented a mechanistic reductionism in which a notion of the self as becoming was undermined by a notion of the self as complex mechanistic activity.

⁴⁵⁷ Rose, Nikolas. "Assembling the Modern Self." In *Rewriting the Self: Histories from the Renaissance to the Present*. Edited by Roy Porter, 224-248. London: Routledge, 1997. See also, Rose, Nikolas. *Inventing Our Selves: Psychology, Power and Personhood*. Cambridge: Cambridge University Press, 1996.

⁴⁵⁸ See e.g., Haraway, Donna. "A Cyborg Manifesto: Science, Technology, and Socialist-Feminism in the Late Twentieth Century." In *Simians, Cyborgs and Women: The Reinvention of Nature*, 149-181. New York: Routledge, 1991; Hacking, Ian. "Canguilhem Amid the Cyborgs." *Economy and Society*, 27;2-3(1998):202-216; Turkle, Sherry. *The Second Self: Computers and the Human Spirit*, Twentieth Anniversary Edition. Cambridge, MA: The MIT Press, 2005.

Epilogue

This dissertation follows a neurophysiological journey through different interpretations and representations of nervous system functionality, and, ultimately, through changing representations of the self. It explores the history of electrophysiological studies of the nervous system and concludes with a reflection on models of the "becoming brain" as physiological models of cognition. It shows how an electroconductive model of nervous system functionality, originating in the mid-nineteenth century, framed twentieth-century neurobiological explanations of perception, learning, memory, language, and intelligent thought and behavior—including those informed by wartime cybernetic theories of communication and control—through the twentieth century. Emil du Bois-Reymond, Herman van Helmholtz, Charles Sherrington, Edgar Adrian, and generations of neurophysiologists helped establish the paradigm of nervous system functionality grounded in the movement of electric current through their electrophysiological experiments on nerves and muscles. By the mid-twentieth century, following the success of the Hodgkin-Huxley conductance-based model, scientists took the electrical conductance paradigm for granted.⁴⁵⁹

⁴⁵⁹ At midcentury the field also reconciled a decades-long debate about the role of chemical transmission in nervous system functionality by reaching consensus about the interaction of electrical and chemical signaling throughout the nervous system via the combined notion of electrochemical transmission. The history of the "soup vs. spark" debate is well documented and is not covered here. Histories of chemical neurotransmitters can be found in histories of psychopharmacology. See e.g., Valenstein, Elliot S. *The War of the Soups and the Sparks: The Discovery of Neurotransmitters and the Dispute Over How Nerves Communicate.* New York: Columbia University Press, 2006; Shorter, Edward. *Before Prozac: The Troubled History of Mood Disorders in Psychiatry.* New York: Oxford University Press, 2009; Healy, David. *The Creation of Psychopharmacology.* Cambridge, MA: Harvard University Press, 2002.

Movement of electricity in the nervous system underwrote neuroscientific concepts of brain and mind functionality, including neuropsychological theories like Hebb's theory of learned behavior as neurophysiological change, providing a physical legitimacy and authority for reinforcing a material yet probabilistic, cybernetically-informed understanding of human cognition and, consequently, of the formation of the self as relentlessly adaptive and selfgoverning. By the end of the twentieth century, the brain became "an object and target for governing human beings."⁴⁶⁰ As dominant as the neurological model of cognition is today, however, it has not completely overwhelmed psychological and psychiatric analysis, nor the philosophy of mind. It is also important to remember that the idea of memory as information writing in a book or on a wax tablet, for example—has a long history which is not covered here.⁴⁶¹

In the early years of the twentieth century, the British neurophysiologist Charles Sherrington, whose support of the neuron doctrine helped cement its widespread acceptance, envisioned the ideal brain as a peak performer, propelled by an evolutionary drive toward optimization.⁴⁶² Sherrington's explicit avowal of Darwinian and Spencerian evolutionary frameworks for organic progress might not be found in the writings of his immediate successors, but the neuroscientific imperative for making our current and future selves better remains within the contemporary drive for understanding the biological basis of learning, memory, and

⁴⁶⁰ Rose, Nikolas, and Joelle Abi-Rached. "Governing Through the Brain: Neuropolitics, Neuroscience and Subjectivity." *The Cambridge Journal of Anthropology*, 32;1(2014):3-23, p. 3.

⁴⁶¹ See e.g., Draaisma, Douwe. *Metaphors of Memory: A History of Ideas About the Mind*. Translated by Paul Vincent. Cambridge: Cambridge University Press, 2000.

⁴⁶² For an explanation of the neuron doctrine debate (i.e., whether or not neurons are independent units), see Finger, Stanley. "Santiago Ramón y Cajal: From Nerve Nets to Neuron Doctrine." In *Minds Behind the Brain: A History of the Pioneers and Their Discoveries*, 197-216. New York: Oxford University Press, 2004; Clarke, Edwin, and L. S. Jacyna. "The Nerve Cell." In *Nineteenth-Century Origins of Neuroscientific Concepts*, 58-100. Berkeley: University of California Press, 1987.

cognition. Inquiries into the meaning of neurobiological conceptions of memory shape and reflect Western morals of an ideal human self.

This dissertation raises several questions about the relationship between neuroscience research and the perceived epidemic of aging. How has memory research reinforced the modern dread of old age? Does senility as a cultural problem serve to maintain a balance of power, privileging biomedical research programs—which have not yet provided effective treatment options for dementia—over other ways of understanding old age and memory loss? The French philosopher and physician Georges Canguilhem reflected on how physiologists impart value judgments when delineating some observed physiological phenomena as error, as they rely on societally-defined, and thus subjective, concepts of normality.⁴⁶³ Neuroscientists' preoccupation with understanding the nervous system in order to control it points to a pervasive cultural need for delineating normality and realizing ideal ways of being which continue to shape cultural norms in the twenty-first century.

Only beginning in the twentieth century did the term dementia evoke associations with old age.⁴⁶⁴ The history of neurophysiology research and ideas about nervous system change can help situate the current Western cultural fear of memory loss toward the end of life. In the mid-nineteenth century, Western clinical observers and experimenters of memory began to investigate how memory broke down in psychiatric patients with memory deficits in order to understand how healthy mechanisms went awry. Soon, maladies of memory became pathological.⁴⁶⁵

⁴⁶³ Canguilhem, Georges. "A New Concept in Pathology: Error." In *The Normal and the Pathological*. Translated by Carolyn R. Fawcett and Robert S. Cohen, 275-287. New York: Zone Books, 1989.

⁴⁶⁴ Berrios, G. E. "Alzheimer's Disease: A Conceptual History." *International Journal of Geriatric Psychiatry*, 5(1990):355-365.

 ⁴⁶⁵ Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996.

By the end of the nineteenth century, clinicians and pathologists referred to dementia primarily as a disorder of cognitive function, defined almost entirely as memory decline.⁴⁶⁶ By World War I, mnestic deficits were the central feature of dementia. Memory was the only cognitive function with adequately developed psychometry; cognition as a whole was too hard to assess or measure. As a result, the dominant paradigm for understanding dementia became intellectual impairment that is often seen as a disability.⁴⁶⁷ Meanwhile, sociological studies placed memory as symbolic for knowledge about ourselves, both as individuals and as nations.

In conversation with the controversy about whether the nervous system consisted of individual units called neurons, pathologists in the early 1900s like the German clinician Alois Alzheimer (1864-1915) attempted to situate their methods as useful in identifying neurological markers of psychiatric disease. Using novel histological staining techniques on postmortem brain tissue, Alzheimer described the defining pathological features of dementia as widespread neuronal loss and the presence of plaques and tangles in the cortex. The neuropathological classification of dementia reinforced the cognitive paradigm and diagnostic instruments largely ignored its noncognitive symptoms, which were psychologically complex and hard to operationalize, until about the 1980s.⁴⁶⁸

⁴⁶⁶ Berrios, G. E. "Alzheimer's Disease: A Conceptual History." *International Journal of Geriatric Psychiatry*, 5(1990):355-365.

⁴⁶⁷ Berrios said the clinical scope of dementia narrowed beginning in the 1860s; the "cognitive paradigm" consolidated by the early 1900s. Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996.

⁴⁶⁸ Berrios, G. E. "Alzheimer's Disease: A Conceptual History." *International Journal of Geriatric Psychiatry*, 5(1990):355-365; Berrios, G. E. "Non-Cognitive Symptoms and the Diagnosis of Dementia: Historical and Clinical Aspects." *British Journal of Psychiatry*, 154;4(1989):11-16; Ramirez-Bermudez, Jesus. "Alzheimer's Disease: Critical Notes on the History of a Medical Concept." *Archives of Medical Research*, 43(2012):595-599; Burns, Alistair. "Another Nail in the Coffin of the Cognitive Paradigm of Dementia." *The British Journal of Psychiatry*, 194(2009):199-200.

Alois Alzheimer's framing of the "cortex pathology" of dementia also might be considered in opposition to brain localization approaches to studying nervous system function and dysfunction.⁴⁶⁹ His observation of widespread postmortem cortical decay in people with dementia provided early support for the diffuseness of memory, and cognition generally, across the nervous system. It is unclear, however, whether neuropathological evidence stemming from the cognitive paradigm of dementia factored into subsequent theories purporting memory as distributed in the brain.

In the 1980s, the Western biomedical establishment transitioned in terminology, replacing senility with Alzheimer's disease as an attempt to reduce stigma. Yet, the fear of memory loss and identity experienced through dementia remains. Senility was not always a bad thing. Not until the late nineteenth century did people in the U.S. come to loathe loss of memory and intellect. The historian Jesse Ballenger traced the changes in U.S. culture and social order which shaped the dread of dementia since the antebellum period. A deterioration of hierarchical social relations diminished the role of the old person in society and aging came to be seen as a loss of self-control while culture shifted toward prizing individuality and willful self-construction. Beginning in the late 1960s, dementia moved from being a pathology of normal aging to a distinct disease as gerontologists and psychiatrists raised awareness and turned towards biomedical science to distinguish between the normal and the pathological. Naming it the "funeral that never ends," Ballenger argued that Alzheimer's disease calls into question personhood, which taps into our worst fears.⁴⁷⁰

⁴⁶⁹ Keuck, Lara. "Slicing the Cortex to Study Mental Illness: Alois Alzheimer's Pictures of Equivalence." In *Vital Models: The Making and Use of Models in the Brain Sciences*. Edited by Tara Mahfoud, Sam McLean, and Nikolas Rose, 25-51. Cambridge, MA: Elsevier, 2017.

⁴⁷⁰ Ballenger, Jesse F. *Self, Senility, and Alzheimer's Disease in Modern America: A History*. Baltimore: Johns Hopkins University Press, 2006, p. 158.

This dissertation details how normal nervous system functionality was established. Looking at a disability like Alzheimer's disease helps reveal the contours of our understanding of normal functioning. In a theory outlined in his book *Stigma*, the sociologist Erving Goffman described the uncertain status of a stigmatized individual who might engage in self-hate and selfderogation because of an inability to conform to society's norms. He said that stigmatized people have spoiled identities and they might attempt to correct their failings in order to gain social acceptance. However, what we collectively label as "acceptable" is constantly changing, and depends on the context. According to Goffman, in order to understand a stigmatized group's place in the social structure, we need to know the history, political development, and current policies of the stigmatized group.⁴⁷¹

The perceived epidemic of Alzheimer's disease cannot be attributed entirely to the biomedical establishment; it is reinforced by cultural norms, and re-reinforced again by biomedicine. In the West, Alzheimer's disease marks a decay of the body, and brings out anxieties about threats to one's autonomy, the unfairness of illness, and the burden on younger generations. The medical anthropologist Lawrence Cohen showed that in northeast India, research on aging reflects the complex understanding of senility as a gendered concept and resulting from a degeneration of the extended family. In the U.S., research focuses on the cognitive aspects of Alzheimer's disease, reflecting a strong cultural tie between memory and cognitive function. In India, behavioral and attitudinal change help mark pathological aging, reflecting cultural ties between memory, emotion and desire. In both places, old people are different, and modern people see that as a problem.⁴⁷²

⁴⁷¹ Goffman, Erving. *Stigma: Notes on the Management of a Spoiled Identity*. New York: Simon and Schuster, 1963.

⁴⁷² Cohen, Lawrence. *No Aging in India: Alzheimer's, the Bad Family, and Other Modern Things*. Berkeley, University of California Press, 1998.

The contemporary meaning of dementia sits at the juncture between neurobiological meaning and cultural meaning. The meaning of dementia, therefore, must be contextualized around the rising influence of neuroscientific concepts which have reinforced a molecularization of morality. The meaning of dementia must also be understood from the perspective of caregivers and people with the disease who experience and express their identities in varied ways. Listening to people with dementia helps us understand how disease affects identity and might help us reframe our understanding of memory as essential to identity.⁴⁷³ If the capacities to learn and remember are no longer taken for granted as defining features of normal nervous systems, what adjustments would neural modelers have to make? Our past and current conceptions about old age and senility have been taken for granted, but they should not have been. In their struggle to understand memory and memory loss, neuroscientists have overlooked that what old age and senility have represented over time and place have been carefully constructed (though often without recourse or attention to the potential consequences) by interested parties within cultural environments that embrace and fortify such representations.

Beginning in the nineteenth century and through the mid-twentieth century, Western ideological persuasions focused on using rationalist knowledge to influence the process of

⁴⁷³ See e.g., Beard, R. L. "In their Voices: Identity Preservation and Experiences of Alzheimer's Disease." Journal of Aging Studies, 18;4(2004):415-428; Bitenc, Rebecca. Reconsidering Dementia Narratives: Empathy, Identity and Care. New York: Routledge, 2020; Degnen, Cathrine. "Ethnographies of Ageing." In Routledge Handbook of Cultural Gerontology. Edited by Julia Trigg and Wendy Martin, 115-112. New York: Routledge, 2015; Dumit, Joseph. Picturing Personhood. Brain Scans and Biomedical Identity. Princeton: Princeton University Press, 2004; Hacking, Ian. Mad Travelers: Reflections on the Reality of Transient Mental Illnesses. University of Virginia Press, 1998; Hydén, Lars-Christer. Entangled Narratives: Collaborative Storytelling and the Re-Imagining of Dementia. Oxford: Oxford University Press, 2017; Kaufman, Sharon R. "'Losing My Self': A Poet's Ironies and a Daughter's Reflections on Dementia." Perspectives in Biology and Medicine, 60;4(2017):549-568; Leibing, Annette, and Lawrence Cohen (eds.). Thinking about Dementia: Culture, Loss, and the Anthropology of Senility. New Brunswick: Rutgers University Press, 2006; Moser, Ingunn. "Dementia and the Limits to Life: Anthropological Sensibilities, STS Interferences, and Possibilities for Action in Care." Science, Technology, & Human Values, 36;5(2011):704-722; Porter, Roy. A Social History of Madness: Stories of the Insane. London: Orion Books, 1996; Robbins, Jessica. "Expanding Personhood Beyond Remembered Selves: The Sociality of Memory at an Alzheimer's Center in Poland." Medical Anthropology Quarterly, (2019):1-18.

individual and societal self-construction. The German philosopher Martin Heidegger (1889-1976) critiqued modernist rationalism as constantly trying to reduce entities to objects to be controlled or resources to be optimized; he saw ourselves as integrally intertwined and mutually determined with the world. Although rejecting their reductionism, his thought was informed by reductionist memory studies, which elicited new philosophical questions about the self and the nature of being.⁴⁷⁴ How concepts emanating from philosophy and psychology shape Western cultural conceptions of the self serve as a starting point for understanding how neurophysiological studies contribute to, reinforce, and change these cultural conceptions over time.

The historian Dorothy Porter demonstrated how new models of prevention emphasizing individual responsibility for health behavior and outcomes in liberal democracies have changed the idea of health citizenship in the twentieth century.⁴⁷⁵ This dissertation, like Porter's work, engages with the question of how we might consider the influence of scientific rationalism upon ideological and cultural transformations of citizenship. The historian Donna Haraway argued that we can arrive at something resembling objectivity only by including partial perspectives and collective and subjective embodied accounts of the truth.⁴⁷⁶ The notion that collective knowledges contribute to the whole truth can be appropriated by scientists, historians, and all those who want to draw from multiple and disparate sources to achieve the whole story about how we arrived at a particular state of knowledge.

⁴⁷⁴ Heidegger, Martin. "The Origin of the Work of Art." In the essay collection, *Holzweg*. Translated under the title, *Off the Beaten Track* by Julian Young and Kenneth Hayes. Cambridge: Cambridge University Press, 2002; Heidegger, Martin. "The Question Concerning Technology." Translated into English 1977.

⁴⁷⁵ Porter, Dorothy. *Health Citizenship: Essays in Social Medicine and Biomedical Politics*. Berkeley: University of California Medical Humanities Press, 2011.

⁴⁷⁶ Haraway, Donna. "Situated Knowledges: The Science Question in Feminism and the Privilege of Partial Perspective." *Feminist Studies*, 14;3(1988):575-599.

G. H. Mead said that minds are constructed by interacting with other minds through the structure of society. Neurophysiologically-inspired neural models do not model interactions between people. This work also raises the question of whether reductionist studies have failed to account for sociological components of the self, and opens up a space for exploring how we might redeem neuroscientific studies of learning, memory and cognition from purely material analysis. If we reconsider, for example, the notion of autonomy as fundamentally relational as opposed to individualistic, neural modelers of cognition would have to consider mentalities as formed within the contexts of social relationships and as shaped by social determinants like race, class, gender, ethnicity, and geography. Accounting for the minds of people as socially embedded forces us to link sociological ideas with the ideas of self-determination and selfgovernment which already constitute the Western meaning of autonomy. Thinking of "autonomy as a characteristic of agents who are emotional, embodied, desiring, creative, and feeling, as well as rational creatures," can highlight the ways individual nervous systems are differentiated from others, but also can inspire new ways of representing the external environment in neural models, for example.⁴⁷⁷ Certain communities provide enriching social environments to foster healthy aging. Experimental studies and alternative care models point to the possibilities of community living for improving memory.⁴⁷⁸ Coding the social aspect of humanity into neural models might require a dramatic restructuring of conceptual assumptions, like that cognition entails continual learning and memory processing through the adjustment of synaptic connections at the microstructural level, for example.

⁴⁷⁷ Mackenzie, Catriona and Natalie Stoljar. "Introduction: Autonomy Refigured." In *Relational Autonomy: Feminist Perspectives on Autonomy, Agency, and the Social Self.* Edited by Catriona Mackenzie and Natalie Stoljar,
3-31. New York: Oxford University Press, 2000, p. 21.

⁴⁷⁸ Haeusermann, Tobias. "Caring Communities." The Postgraduate Journal of Medical Humanities, 2(2015):61-83.

The question of the nature of the relationship between neurobiology and cognition raises the larger cultural question of what it means to be human. International discourse and research into the neurobiology of cognition informed and was informed by cultural understandings of cognition and the self. A nineteenth-century conception of the action current as an altered state of electromotive force, made possible by an epistemological shift in thinking about the past in order to understand the present, was replaced by a more sophisticated materialist model of electroconductivity beginning in the early twentieth century. This newer physiological notion of what constitutes behavior was challenged at midcentury by the neuropsychological theory of behavior presented by Hebb, who understood the purely material analysis of behavior as inadequate. His theory about the neural correlates of behavior and thought and how they necessarily change through the processes of learning and memory inscribed thought as a form of social history and paralleled Mead's model of meaning as emerging from symbolic interactionism. New models of cognition as computation, emerging from cybernetic and information theory and probabilistic mathematics, were a return to a mechanistic philosophy despite incorporating Hebbian principles of synaptic plasticity.

A physiological conceptualization of cognition as emerging from moving electric current which restructures our material being profoundly shapes the essence of what it means to live as a human being today. Accepting cognition as fundamentally mediated by electroconductive functional processes can, at times, lead us to forget that a brain is more than something that acts on objects amidst an incessantly-changing milieu. This dissertation charts the course of shifting neuroscientific paradigms over more than a century, culminating in notions of brain functionality as in fluidity, as in an unrelenting process of becoming by the late twentieth century. This dissertation asks neuroscientists, scholars, policymakers, and society at large not to focus on

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human selves solely as actors, constantly performing and adapting, but on other ways of being which do not demand the persistent pursuit of becoming.

References

Archival Collections

A. L. Hodgkin papers, Trinity College Archive, University of Cambridge, Cambridge, England.
Bernard Katz papers, University College London, London, England.
Donald Olding Hebb fonds, McGill University Archives, Montreal, Quebec, Canada.
J. Z. Young papers, University College London, London, England.
Norbert Wiener papers, MIT Distinctive Collections, Cambridge, MA, USA.

Primary Sources

- Adrian, E. D. "Some Recent Work on Inhibition." Brain, 47;4(1924):399-416.
- Adrian, E. D. "The Analysis of the Nervous System." Proceedings of the Royal Society of Medicine, 50(1957):991-998.
- Adrian, E. D. and D. W. Bronk. "The Discharge of Impulses in Motor Nerve Fibres. Part II. The Frequency of Discharge in Reflex Voluntary Contractions." *The Journal of Physiology*, 67;2(1929):119-151.
- Adrian, E. D. and D. W. Bronk. "The Discharge of Impulses in Motor Nerve Fibres. Part II. The Frequency of Discharge in Reflex Voluntary Contractions." *The Journal of Physiology*, 67;2(1929):119-151.
- Adrian, E. D. *The Basis of Sensation: The Action of the Sense Organs*. London: Christopher, 1928.

- Adrian, E. D., and Keith Lucas. "On the Summation of Propagated Disturbances in Nerve and Muscle." *The Journal of Physiology*, 44;1-2(1912):68-124.
- Adrian, Edgar D. "The All-or-None Principle in Nerve." *The Journal of Physiology*, 47;6 (1914):460-474.
- Adrian, Edgar D. "The All-or-None Principle in Nerve." *The Journal of Physiology*, 47;6(1914):460-474.
- Adrian, Edgar D. *The Mechanism of Nervous Action*. Philadelphia: University of Pennsylvania Press, 1932.
- Angell, James R. "A Reconsideration of James's Theory of Emotion in the Light of Recent Criticisms." *Psychological Review*, 23;4(1916):251-261.
- Arbib, Michael. Brains, Machines, and Mathematics. New York: McGraw Hill, 1964.
- Arbib, Michael. *The Metaphorical Brain: An Introduction to Cybernetics as Artificial Intelligence and Brain Theory.* New York: Wiley Interscience, 1972.
- Ashby, W. Ross. Design for a Brain: The Origin of Adaptive Behavior. New York: John Wiley & Sons, 1960.
- Bain, Alexander. Mind and Body: The Theories of Their Relation. London: Henry S. King, 1872.
- Bartlett, F. C. *Remembering: A Study in Experimental and Social Psychology*. Cambridge: Cambridge University Press, 1932.
- Beard, George M. and A. D. Rockwell, "Electro-Physiology Animal Electricity." In A Practical Treatise on the Medical and Surgical Uses of Electricity including Localized and General Electrization. New York: William Wood & Co., 1871.
- Bergson, Henri. *Creative Evolution*. Translated by Arthur Mitchell. New York: Henry Holt and Company, 1911.

- Bergson, Henri. *Matter and Memory*. Translated by Nancy Margaret Paul and W. Scott Palmer. New York: The Macmillan Company, 2005.
- Bergson, Henri. *Time and Free Will: An Essay on the Immediate Data of Consciousness*. Translated by F. L. Pogson. New York: The MacMillan Company, 1913.
- Bliss, T. V., and T. Lømo. "Long-Lasting Potentiation of Synaptic Transmission in the Dentate Area of the Anaesthetized Rabbit Following Stimulation of the Perforant Path." *The Journal of Physiology*, 232;4(1973):331-356.

Bode, H. W. Network Analysis and Feedback Amplifier Design, New York: Nostrand, 1945.

- Bradley, J. K., and E. M. Tansey. "The Coming of the Electronic Age to the Cambridge Physiology Laboratory: E. D. Adrian's Valve Amplifier in 1921." *Notes and Records of the Royal Society of London*, 50;2(1996):217-228.
- Brazier, Mary A. B. (ed.). The Central Nervous System and Behavior. Transactions of the First Conference – February 23, 24, 25, and 26, 1958. Madison, NJ: Madison Printing Co., Inc., 1959.
- Calkins, Mary Whiton. "A Reconciliation Between Structural and Functional Psychology." *Psychological Review*, 13(1906):61-81.
- Canguilhem, Georges. *The Normal and the Pathological*. Translated by Carolyn R. Fawcett and Robert S. Cohen. New York: Zone Books, 1989.
- Cannon, Walter B. "Organization for Physiological Homeostasis." *Physiological Reviews*, 9;3(1929):399-431.

Cannon, Walter B. *The Wisdom of the Body*. New York: W. W. Norton & Company, 1932. Chomsky, Noam. *The Logical Structure of Linguistic Theory*. New York: Springer, 1975.

- Creed, Richard Stephen, Denny-Brown, Derek, Eccles, John Carew, Liddell, Edward George Tandy, and Charles Scott Sherrington. *Reflex Activity of the Spinal Cord*. London: Oxford University Press, 1932.
- Davis, Hallowell. "The Forbes 'School' of Neurophysiology at Harvard." Electroencephalography and Clinical Neurophysiology, 1;2(1949):139-140.
- Denny-Brown, D. "The Sherrington School of Physiology." *Journal of Neurophysiology*, 20(1957):543-548.
- Dionessov, S. M., Eisenberg, A. V., and L. N. Fedorov (eds.). Proceedings of the XVth International Physiological Congress. Leningrad-Moscow, August 9th to 16th, 1935. The Sechenov Journal of Physiology of the USSR, Vol. XXI, No. 5-6. Moscow-Leningrad: State Biological and Medical Press, 1938.
- Draaisma, Douwe. *Metaphors of Memory: A History of Ideas About the Mind*. Translated by Paul Vincent. Cambridge: Cambridge University Press, 2000.
- Du Bois-Reymond, Emil, Jones, H. Bence, and Johannes Müller. *On Animal Electricity: Being an Abstract of the Discoveries of Emil Du Bois-Reymond*. London: Churchill, 1852.
- Du Bois-Reymond, Emil. *Untersuchungen über thierische Elektricität*. Vol. 1 and Part 1, Vol. 2. Berlin: Verlag von G. Reimer, 1848 and 1849.
- Dusser de Barenne, J. G., and Warren S. McCulloch. "Functional Boundaries in the Sensori-Motor Cortex of the Monkey." *Proceedings of the Society for Experimental Biology and Medicine*, 35;2(1936):329-331.
- Faraday, Michael. *Experimental Researches in Electricity*. Volume 1. London: Bernard Quaritch, 1839.

- Fatt, Paul and Bernard Katz. "An Analysis of the End-Plate Potential Recorded with an Intracellular Electrode." *The Journal of Physiology*, 115;3(1951):320-370.
- Fatt, Paul and Bernard Katz. "Spontaneous Subthreshold Activity at Motor Nerve Endings." *The Journal of Physiology*, 117;1(1952):109-128.
- Fleming, J. A. "The Thermionic Valve in Wireless Telegraphy and Telephony." *Nature*, 2649;105(1920):716-720.
- Foerster, Heinz von (ed.). *Cybernetics: Transactions of the Seventh Conference, March 23-24,* 1950. New York: Josiah Macy, Jr. Foundation, 1951.
- Forbes, A. and C. Thacher. "Amplicatoin of Action Currents with the Electron Tube in Recording with the String Galvanometer." *The Journal of Physiology*, 53;3(1920):409-471.
- Forbes, Alexander. "The Interpretation of Spinal Reflexes in Terms of Present Knowledge of Nerve Conduction." *Physiological Reviews*, 2;3(1922):361-414.
- Forbes, Alexander. "The Mechanism of Reaction." In A Handbook of General Experimental Psychology. Edited by Carl Murchison, 155-203. Worcester, MA: Clark University Press, 1934.
- Foucault, Michel. *The Hermeneutics of the Subject: Lectures at the Collège de France 1981– 1982*. Edited by F. Gros, translated by G. Burchell. New York: Palgrave Macmillan, 2007.
- Foucault, Michel. *The History of Sexuality, Vol. 3: The Care of the Self.* Translated by R. Hurley. New York: Random House, 1986.
- Frankenhaeuser, B. "Saltatory Conduction in Myelinated Nerve Fibres." *The Journal of Physiology*, 118;1(1952):107-112.

- Frankenhaeuser, B. and A. L. Hodgkin. "The After-Effects of Impulses in the Giant Nerve Fibres of Loligo." *The Journal of Physiology*, 131(1956):341-376.
- Frankenhaeuser, B. and Dietrich Schneider. "Some Electrophysiological Observations on Isolated Single Myelinated Nerve Fibres (Saltatory Conduction)." *The Journal of Physiology*, 115(1951):177-184.
- Freeman, W., and J. W. Watts. Psychosurgery: Intelligence, Emotion and Social Behavior Following Prefrontal Lobotomy for Mental Disorders, Springfield, IL: Charles C. Thomas, 1942.
- Fulton, J. F. "Sherrington's Impact on Neurophysiology." *British Medical Journal*, (1947):807-810.
- Fulton, J. F. "Sir Charles Scott Sherrington, O.M. (1857-1952)." The Journal of Neurophysiology, 15(1952):167-190.
- Gasser, Herbert S. "The Control of Excitation in the Nervous System." *Bulletin of the New York Academy of Medicine*, 13;6(1937):324-348.
- Gerard, Ralph. "The Activity of Nerve." Science, 66;1717(1927):495-499.
- Gibbs, Josiah Willard. Elementary Principles in Statistical Mechanics: Developed with Special Reference to the Rational Foundation of Thermodynamics. New York: Charles Scribner's Sons, 1902.
- Halbwachs, Maurice. *On Collective Memory*. Edited, translated, and with an introduction by Lewis A. Coser. Chicago: The University of Chicago Press, 1992.
- Hebb, D. O. "A Neuropsychological Theory." In Psychology: A Study of a Science, Study I.
 Conceptual and Systematic. Volume 1. Sensory, Perceptual, and Physiological
 Formulations. Edited by Sigmund Koch, 622-643. New York: McGraw-Hill, 1959.

- Hebb, D. O. "Intelligence in Man After Large Removals of Cerebral Tissue. Report of Four Left Frontal Lobe Cases." *The Journal of General Psychology*, 21(1939):73-87.
- Hebb, D. O. "Man's Frontal Lobes: A Critical Review." *Archives of Neurology and Psychiatry*, 54;1(1945):10-24.
- Hebb, D. O. "On Human Thought." Canadian Journal of Psychology, 7;3(1953):99-110.
- Hebb, D. O. "The Role of Neurological Ideas in Psychology." *Journal of Personality*, 20;1(1951):39-55.
- Hebb, D. O. *The Organization of Behavior: A Neuropsychological Theory*. New York: John Wiley & Sons.
- Hebb, D. O., and W. Penfield. "Human Behavior After Extensive Bilateral Removal from the Frontal Lobes." *Archives of Neurology and Psychiatry*, 44;2(1940):421-438.
- Hegel, Georg Wilhelm Friedrich. "D. Recent Philosophy: Kant, Fichte, Jacobi, Schelling." In Lectures on the History of Philosophy: The Lectures of 1825-26, Vol. III. Edited by Robert F. Brown, translated by Robert F. Brown, J. M. Stewart and H. S. Harris. Berkeley: University of California Press, 1990.
- Heidegger, Martin. "The Origin of the Work of Art." In the essay collection, *Holzweg*.Translated under the title, *Off the Beaten Track* by Julian Young and Kenneth Hayes.Cambridge: Cambridge University Press, 2002.

Heidegger, Martin. "The Question Concerning Technology." Translated into English 1977.

Helmholtz, Hermann von. "On the Application of the Law of the Conservation of Force to Organic Nature." In Notices of the Proceedings at the Meetings of the Members of the Royal Institution of Great Britain with Abstracts of the Discourses Delivered at the *Evening Meetings, Vol. III. 1858-1862*, 347-357. London: William Clowes and Sons, 1862.

- Helmholtz, Hermann von. "On the Conservation of Force; A Physical Memoir." Translated by John Tyndall. In Scientific Memoirs, Selected from the Transactions of Foreign Academies of Science, and from Foreign Journals. Edited by John Tyndall and William Francis, 114-162. London: Taylor and Francis, 1853.
- Helmholtz, Hermann von. "On the Relation of Natural Science and General Science." In *Popular Lectures on Scientific Subjects*. By H. Helmholtz, translated by E. Atkinson, 1-32. New York: D. Appleton and Company, 1885.
- Hill, A. V. "Energy Exchanges in Muscle and Nerve: Myothermic and Nevrothermic Experiments." Archivo di Scienze Biologiche, XIV Congreso Internazionale di Fisiologa Conferenze e Sunti Delle Comunicazioni, 18;1-2-3-4(1933):3-14.
- Hill, A. V. "The Heat Production of Muscle and Nerve, 1848-1914: The First Chapter of a Future Monograph." *Annual Reviews of Physiology*, 21(1959):1-19.
- Hill, A. V. Chemical Wave Transmission. London: Cambridge University Press, 1932.
- Hodgkin, A. L. "Chance and Design in Electrophysiology: An Informal Account of Certain Experiments on Nerve Carried Out Between 1934 and 1952." *The Journal of Physiology*, 263;1(1976):1-22.
- Hodgkin, A. L. "Evidence for Electrical Transmission in Nerve." *The Journal of Physiology*, 90;2(1937):183-210.
- Hodgkin, A. L. "The Croonian Lecture Ionic Movements and Electrical Activity in Giant Nerve Fibres." *Proceedings of the Royal Society of London B*, 148;930(1958):1-37.

- Hodgkin, A. L. "The Effect of Potassium on the Surface Membrane of an Isolated Axon." *The Journal of Physiology*, 106(1947):319-340.
- Hodgkin, A. L. *Chance and Design: Reminiscences of Science in Peace and War*. Cambridge: Cambridge University Press, 1992.
- Hodgkin, A. L. *The Conduction of the Nervous Impulse*. Liverpool: Liverpool University Press, 1967.
- Hodgkin, A. L., and A. F. Huxley. "A Quantitative Description of Membrane Current and its Application to Conduction and Excitation in Nerve." *The Journal of Physiology*, 117(1952):500-544.
- Hodgkin, A. L., and A. F. Huxley. "Action Potentials Recorded from Inside a Nerve Fibre." *Nature*, 144(1939):710-711.
- Hodgkin, A. L., and A. F. Huxley. "Currents Carried by Sodium and Potassium Ions Through the Membrane of the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952): 449-472.
- Hodgkin, A. L., and A. F. Huxley. "The Components of Membrane Conductance in the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):473-496.
- Hodgkin, A. L., and A. F. Huxley. "The Dual Effect of Membrane Potential on Sodium Conductance in the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):497-506.
- Hodgkin, A. L., and B. Katz. "The Effect of Sodium Ions on the Electrical Activity of Giant Axon of the Squid." *The Journal of Physiology*, 108(1949):37-77.
- Hodgkin, A. L., Huxley, A. F., and B. Katz. "Measurement of Current-Voltage Relations in the Membrane of the Giant Axon of Loligo." *The Journal of Physiology*, 116(1952):424-448.

- Hogdkin, A. L., and A. F. Huxley. "Potassium Leakage from an Active Nerve Fibre." *Nature*, 158(1946):376-377.
- Hopfield, J. J. "Neural Networks and Physical Systems with Emergent Collective Computational Abilities." *Proceedings of the National Academy of Sciences of the United States of America*, 79(1982):2554-2558.
- Hubel, D. H., and T. N. Wiesel. "Receptive Fields and Functional Architecture in Two Nonstriate Visual Areas (18 and 19) of the Cat." *Journal of Neurophysiology*, 28;2(1965):229-289.
- Hubel, D. H., and T. N. Wiesel. "Receptive Fields and Functional Architecture of Monkey Striate Cortex." *The Journal of Physiology*, 195;1(1968):215-243.
- Hubel, D. H., and T. N. Wiesel. "Receptive Fields, Binocular Interaction and Functional Architecture in the Cat's Visual Cortex." *The Journal of Physiology*, 160;1(1962):106-154.
- Hubel, D. H., and T. N. Wiesel. Brain and Visual Perception: The Story of a 25-Year Collaboration. New York: Oxford University Press, 2005.
- Hull, Clark L. "Introduction to an Objective Theory of Behavior" and "Stimulus Reception and Organism Survival." In *Principles of Behavior: An Introduction to Behavior Theory*, 16-49. New York: Appleton-Century-Crofts, 1943.
- Hull, Clark L. *Principles of Behavior: An Introduction to Behavior Theory*. New York: Appleton-Century-Crofts, 1943.
- Huxley, A. F. "Electrical Activity in Nerve: The Background up to 1952." In *The Axon: Structure, Function and Pathophysiology*. Edited by S. G. Waxman, J. D. Kocsis, and P. K. Stys, 3-10. New York: Oxford University Press, 1995.

- Huxley, A. F. and R. Stämpfli. "Evidence for Saltatory Conduction in Peripheral Myelinated Nerve Fibres." *The Journal of Physiology*, 108;3(1949):315-339.
- Jackson, John Hughlings. "The Croonian Lectures on Evolution and Dissolution of the Nervous System. Lecture II." *The British Medical Journal*, 1;1214(1884):660-663.
- Jackson, John Hughlings. "The Croonian Lectures on Evolution and Dissolution of the Nervous System. Lecture III." *The British Medical Journal*, 1;1217(1884):739-744.
- Jackson, John Hughlings. *Selected Writings of John Hughlings Jackson*, Vol. 1. Edited by J. Taylor. London: Hodder & Stoughton, 1931.
- James, William. *A Pluralistic Universe*. Edited by Ralph Barton Perry. New York: E. P. Dutton, 1909.
- James, William. *The Principles of Psychology*, Vol.1. New York: Henry Holt and Company, 1890.
- Jelved, Karen, and Hans Christian Ørsted. *Selected Scientific Works of Hans Christian Orsted*. Edited by Andrew D. Jackson and Ole Knudsen. Princeton: Princeton University Press, 1998.
- Jones, H. Bence. The Life and Letters of Faraday. Volume 2. Philadelphia: Lippincott, 1870.
- Kandel, Eric R. *In Search of Memory: The Emergence of a New Science of Mind*. New York: W.W. Norton & Company, 2006.

 Kato, G. "On the Excitation, Conduction, and Narcotisation of Single Nerve Fibres." *Cold* Spring Harbor Symposium on Quantitative Biology – Excitation Phenomena, 4(1936):202-213.

Kato, G. *The Theory of Decrementless Conduction in Narcotised Region of Nerve*. Tokyo: Nankōdō, Hongo, 1924.

- Katz, Bernard. "Bayliss-Starling Memorial Lecture (1985): Reminiscences of a Physiologist, 50Years After." *The Journal of Physiology*, 370(1986):1-12.
- Katz, Bernard. "Sir Bernard Katz." In *The History of Neuroscience in Autobiography*, Vol 1.Edited by Larry R. Squire, 348-381. Washington, DC: Society for Neuroscience, 1996.

Katz, Bernard. Nerve, Muscle, and Synapse. New York: McGraw-Hill, 1966.

- Katz, Bernhard. "Experimental Evidence for a Non-Conducted Response of Nerve to Subthreshold Stimulation." *Proceedings of the Royal Society B*, 124;835(1937):244-276.
- Kaufman, Sharon R. "'Losing My Self': A Poet's Ironies and a Daughter's Reflections on Dementia." *Perspectives in Biology and Medicine*, 60;4(2017):549-568.
- Köhler, Wolfgang. "Gestalt Psychology Today." American Psychologist, 14;12(1959):727-734.

Köhler, Wolfgang. Dynamics in Psychology. New York: Liveright, 1940.

Köhler, Wolfgang. Gestalt Psychology. New York: Horace Liveright, 1929.

- Köhler, Wolfgang. *The Mentality of Apes*. Translated by Ella Winter. New York: Harcourt, Brace and Co., 1925.
- Lashley, K. S. "Basic Neural Mechanisms in Behavior." *Psychological Review*, 37;1(1930):1-24.
- Lashley, K. S. "Cerebral Organization and Behavior." *Proceedings of the Association for Research in Nervous and Mental Diseases*, 36(1958):1-18.
- Lashley, K. S. "Coalescence of Neurology and Psychology." *Proceedings of the American Philosophical Society*, 84;4(1941):461-470.
- Lashley, K. S. "The Behavioristic Interpretation of Consciousness I and II." *Psychological Review*, 30;4&5(1923):237-272, 329-353.
- Lashley, K. S. "The Mechanism of Vision XV. Preliminary Studies of the Rat's Capacity for Detail Vision." *The Journal of General Psychology*, 19(1938):123-193.

- Lashley, K. S. and M. Wade. "The Pavlovian Theory of Generalization." *Psychological Review*, 53;2(1946):72-87.
- Lashley, K. S. *Brain Mechanisms and Intelligence: A Quantitative Study of Injuries to the Brain.* Chicago: University of Chicago Press, 1929.
- Lashley, K. S. The Neuropsychology of Lashley: Selected Papers of K. S. Lashley. Edited by Frank A. Beach, Donald O. Hebb, Clifford T. Morgan and Henry W. Nissen. New York: McGraw-Hill.
- Leeper, Robert. "The Relation Between Gestalt Psychology and the Behavioristic Psychology of Learning." *Transactions of the Kansas Academy of Science*, 34(1931):268-273, 269.
- Lettvin, J. Y. et al. "What the Frog's Eye Tells the Frog's Brain." *Proceedings of the IRE*, 47;11(1959):1940-1959.
- Lillie, R. S. "Factors Affecting Transmission and Recovery in the Passive Iron Nerve Model." Journal of General Physiology, 7;4(1925):473-507.
- Lorente de Nó, Rafael. "Observations on the Properties of the Epineurium of the Frog Nerve." *Cold Spring Harbor Symposium on Quantitative Biology – The Neuron*, 17(1952):299-315.
- Lucas, Keith. "Croonian Lecture: The Process of Excitation in Nerve and Muscle." *Proceedings* of the Royal Society of London B, 85;582(1912):495-524.
- Lucas, Keith. "On the Gradation of Activity in a Skeletal Muscle-Fibre." *The Journal of Physiology*, 33;2 (1905):125-137.
- Lucas, Keith. "On the Rate of Variation of the Excitation Current as a Factor of Electric Excitation." *The Journal of Physiology*, 36;4-5(1907):253-274.

- Lucas, Keith. "On the Refractory Period of Muscle and Nerve." *The Journal of Physiology*, 39;5 (1909):331-340.
- Lucas, Keith. "The Excitable Substances of Amphibian Muscle." *The Journal of Physiology*, 36;2-3(1907):113-135.

Lucas, Keith. The Conduction of the Nervous Impulse. London: Longmans, Green and Co., 1917.

- MacKay, Donald M., and Warren McCulloch. "The Limiting Information Capacity of a Neuronal Link." *The Bulletin of Mathematical Biophysics*, 14;2(1952):127-135.
- Marmont, M. "Studies on the Axon Membrane I. A New Method." *Journal of Cellular and Comparative Physiology*, 34;3(1949):351-382.
- Matteucci, Carlo "Electro-Physiological Researches First Memoir. The Muscular Current." *Philosophical Transactions of the Royal Society of London*. Part I. Communicated by Michael Faraday, 283-296. London: Richard and John E. Taylor, 1845
- McClelland, James L. "Memory as a Constructive Process: The Parallel Distributed Processing Approach." In *The Memory Process: Neuroscientific and Humanistic Perspectives*.
 Edited by S. Nalbantian, P. M. Matthews, & J. L. McClelland, 129-155. Cambridge, MA: The MIT Press, 2011.
- McClelland, James L., Rumelhart, David E. and the PDP Research Group. *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 2: Psychological and Biological Models*. Cambridge, MA: The MIT Press, 1986.
- McCulloch, Warren S. "What is a Number, that a Man May Know It, and a Man, that he May Know a Number?" *General Semantic Bulletin*, 26-7(1960):7-18.

McCulloch, Warren S. Embodiments of Mind. Cambridge, MA: The MIT Press, 1965.

- McCulloch, Warren S., and Walter Pitts. "A Logical Calculus of the Ideas Immanent in Nervous Activity." *Bulletin of Mathematical Biophysics*, 5(1943):115-133.
- McDougall, W. "The Nature of Inhibitory Processes Within the Nervous System." *Brain*, 26;2(1903):153-219.
- Mead, George Herbert. "The Genesis of the Self and Social Control." *International Journal of Ethics*, 35;3 (1925):251-277.
- Mead, George Herbert. *Mind, Self and Society from the Standpoint of a Social Behaviorist.* Edited by Charles W. Morris. Chicago: University of Chicago Press, 1934.
- Minsky, M. "Steps Toward Artificial Intelligence." Proceedings of the IRE, 49;1(1961):8-30.
- Minsky, M. and S. Papert. *Perceptrons: An Introduction to Computational Geometry*, Expanded edition. Cambridge, MA: The MIT Press, 1988.
- Morgan, C. E. Electro-Physiology and Therapeutics; Being a Study of the Electrical and Other Physical Phenomena of the Muscular and Other Systems During Health and Disease, Including the Phenomena of the Electrical Fishes. New York: William Wood & Co., 1868.

Neumann, John. The Computer and the Brain. New Haven: Yale University Press, 1958.

- Pavlov, I. P. "The Reply of a Physiologist to Psychologists." *Psychological Review*, 39;2(1932):91-127.
- Pavlov, I. P. Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex. Edited and translated by G. V. Anrep. Oxford: Oxford University Press, 1927.
- Pitts, Walter, and Warren S. McCulloch. "How We Know Universals: The Perception of Auditory and Visual Forms." *Bulletin of Mathematical Biophysics*, 9(1947):127-147.

- Ramón y Cajal, Santiago. "The Croonian Lecture: La Fine Structure des Centres Nerveux." *Proceedings of the Royal Society of London*, 55(1894):444-468;
- Ramón y Cajal, Santiago. *Nuevo Concepto de la Histología de los Centros Nerviosos*. Barcelona: Henrich, 1893.
- Rashbass, C., and W. A. H. Rushton. "The Relation of Structure to the Spread of Excitation in the Frog's Sciatic Trunk." *The Journal of Physiology*, 110(1949):110-135.
- Razran, Gregory. "Stimulus Generalization of Conditioned Responses." *Psychological Bulletin*, 46;5(1949):337-365.
- Ribot, T. H. *Diseases of Memory: An Essay in the Positive Psychology*. London: Kegan Paul, Trench & Co, 1882.
- Rosenblatt, F. "The Perceptron: A Probabilistic Model for Information Storage and Organization in the Brain." *Psychological Review*, 65;6(1958):386-408.
- Rosenblueth, Arturo, Wiener, Norbert, and Julian Bigelow. "Behavior, Purpose and Teleology." *Philosophy of Science*, 10;1(1943):18-24.
- Rumelhart, David E., McClelland, James L., and the PDP Research Group. *Parallel Distributed Processing: Explorations in the Microstructure of Cognition, Volume 1: Foundations.* Cambridge, MA: The MIT Press, 1986.
- Rushton, W. A. H. "Lapicque's Theory of Curarization." *The Journal of Physiology*, 77;4(1933):337-364.
- Russell, Bertrand. Philosophy. New York: W. W. Norton & Company, 1927.
- Russell, Bertrand. The Analysis of Mind. London: George Allen & Unwin, 1921.
- Satō, Shunsuke. "Role and Use of Noise in Biological Systems." In Competition and

Cooperation in Neural Nets: Proceedings of the U.S.-Japan Joint Seminar held at Kyoto,

Japan, February 15-19, 1982. Edited by S. Amari and M.A. Arbib, 111-120. New York: Springer-Verlag, 1982.

- Schneider, Walter. "Connectionism: Is it a Paradigm Shift for Psychology?" *Behavior Research Methods, Instruments & Computers.* 19;2(1987):73-83.
- Schrödinger, Erwin. *What Is Life? The Physical Aspect of the Living Cell and Mind and Matter.* Cambridge: Cambridge University Press, 1944.
- Scoville, William Beecher, and Brenda Milner. "Loss of Recent Memory after Bilateral Hippocampal Lesions." *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1957):11-21.
- Sejnowski, Terrence J. The Deep Learning Revolution. Cambridge, MA: The MIT Press, 2018.
- Shannon, Claude, and Warren Weaver. *The Mathematical Theory of Communication*. Urbana: The University of Illinois Press, 1949.
- Shannon, Claude. "A Mathematical Theory of Communication." *Bell System Technical Journal*, 27;3(1948):379-423.
- Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science, 728-741. London: John Murray, 1905.
- Sherrington, Charles S. "Correlation of Reflexes and the Principle of the Common Path." In Report of the Seventy-Fourth Meeting of the British Association for the Advancement of Science, 728-741. London: John Murray, 1905.
- Sherrington, Charles S. "Experiments on the Value of Vascular and Visceral Factors for the Genesis of Emotion." *Proceedings of the Royal Society of London*, 66(1900):390-403.

- Sherrington, Charles S. "Ferrier Lecture—Some Functional Problems Attaching to Convergence." Proceedings of the Royal Society of London. Series B, Biological Sciences, 105;737(1929):332-362.
- Sherrington, Charles S. "Note Toward the Localisation of the Knee-Jerk." *British Medical Journal*, 1;1628(1892):545.
- Sherrington, Charles S. *Man on his Nature*. The Gifford Lectures, Edinburgh, 1937-1938. New York: The Macmillan Company, 1941.
- Sherrington, Charles S. *The Integrative Action of the Nervous System*. New York: Charles Scribner's Sons, 1906.
- Spence, Kenneth W. "Foreword to the Seventh Printing." In *Principles of Behavior: An Introduction to Behavior Theory*, by Clark L. Hull, vii-xvii. New York: Appleton-Century-Crofts, 1943.
- Spencer, Herbert. "The Functions of the Nervous System." In *The Principles of Psychology*, Vol. I, 48-67. New York: D. Appleton and Company, 1873.
- Spencer, Herbert. *The Principles of Psychology*, Vols. I and II. New York: D. Appleton and Company, 1873.
- Squire, Larry R. (ed.). *The History of Neuroscience in Autobiography*. Volumes 1-8. Washington, DC: Society for Neuroscience, 1996-2014.
- Squire, Larry R., and Thomas D. Albright. (eds.). *The History of Neuroscience in Autobiography*. Volumes 9-11. Washington, DC: Society for Neuroscience, 2016-2020.
- Tasaki, I. "Electric Stimulation and the Excitatory Process in the Nerve Fiber." *American Journal of Physiology*, 125;2(1939):380-395.

Tasaki, I. "The Strength-Duration Relation of the Normal, Polarized and Narcotized Nerve Fiber." *American Journal of Physiology*, 125;2(1939):367-379.

Thorndike, Edward L. Animal Intelligence: Experimental Studies. New York: MacMillan, 1911.

- Titchener, E. B. "On 'Psychology as the Behaviorist Views It."" *Proceedings of the American Philosophical Society*, 53(1914):1-17.
- Titchener, E. B. "Simple Reactions." Mind, 4(1895):74-81.
- Titchener, E. B. "The Postulates of Structural Psychology." *Philosophical Review*, 7(1898):449-465.
- Tyndall, John. "Introduction." In *Popular Lectures on Scientific Subjects*. By H. Helmholtz, translated by E. Atkinson, xv-xvi. New York: D. Appleton and Company, 1885.
- Watson, John B. "Psychology as the Behaviorist Views It." *Psychological Review*, 20(1913):158-177.
- Watson, John B. *Behavior: An Introduction to Comparative Psychology*. New York: Henry Holt, 1914.
- Watson, John B. Behaviorism. New York: Norton, 1924.
- Watson, John B. *Psychology from the Standpoint of a Behaviorist*. Philadelphia: J. B. Lippincott, 1919.
- Wiener, Norbert. *Cybernetics: Or Control and Communication in the Animal and the Machine*. Cambridge, MA: The MIT Press, 1948.
- Wiener, Norbert. *Nonlinear Problems in Random Theory*. Cambridge, MA: The MIT Press, 1958.
- Wiener, Norbert. *The Human Use of Human Beings*. Cambridge, MA: The MIT Press, 1950.Wilson, M. O. "Chronaxie." *Psychological Bulletin*, 32;1(1935):4-32.

Secondary Sources

"The New Anatomy." Nature, 158;4205(1946):907.

- Abir-Am, Pnina Geraldine. "The Biotheoretical Gathering, Trans-Disciplinary Authority and the Incipient Legitimation of Molecular Biology in the 1930s." *History of Science*, 25;1(1987):1-70.
- Abir-Am, Pnina Geraldine. "Themes, Genres and Orders of Legitimation in the Consolidation of New Scientific Disciplines: Deconstructing the Historiography of Molecular Biology." *History of Science*, 23(1985):73-117.
- Abraham, Tara H. "(Physio)logical Circuits: The Intellectual Origins of the McCulloch-Pitts Neural Networks." *Journal of the History of the Behavioral Sciences*, 80;1(2002):3-25.
- Abraham, Tara H. *Rebel Genius: Warren McCulloch's Transdisciplinary Life in Science*. Cambridge, MA: The MIT Press, 2016.
- Allen, Garland. "The History of Evolutionary Thought." In *The Princeton Guide to Evolution*. Edited by Jonathan B. Losos, et al., 10-27. Princeton: Princeton University Press, 2013.
- Archibald, J. David. "Marking Time." In *Origins of Darwin's Evolution: Solving the Species Puzzle Through Time and Place*, 44-58. New York: Columbia University Press, 2017.
- Ballenger, Jesse F. Self, Senility, and Alzheimer's Disease in Modern America: A History.Baltimore: Johns Hopkins University Press, 2006.
- Beard, R. L. "In their Voices: Identity Preservation and Experiences of Alzheimer's Disease." *Journal of Aging Studies*, 18;4(2004):415-428.
- Beiser, Frederick C. "Introduction: Hegel and the Problem of Metaphysics." In *The Cambridge Companion to Hegel*. Edited by Frederick C. Beiser, 1-24. Cambridge: Cambridge University Press, 1993.

- Beiser, Frederick C. German Idealism: The Struggle Against Subjectivism, 1781–1801. Cambridge, MA: Harvard University Press, 2002.
- Berrios, G. E. "Alzheimer's Disease: A Conceptual History." *International Journal of Geriatric Psychiatry*, 5(1990):355-365.
- Berrios, G. E. "Non-Cognitive Symptoms and the Diagnosis of Dementia: Historical and Clinical Aspects." *British Journal of Psychiatry*, 154;4(1989):11-16.
- Berrios, German E. "Cognitive Impairment," "Memory and its Disorders," and "Consciousness and its Disorders." In *The History of Mental Symptoms: Descriptive Psychopathology Since the Nineteenth Century*, 172-260. Cambridge: Cambridge University Press, 1996.
- Berrios, German E., and John Hodges. *Memory Disorders in Psychiatric Practice*. Cambridge: Cambridge University Press, 2000.
- Bitenc, Rebecca. *Reconsidering Dementia Narratives: Empathy, Identity and Care.* New York: Routledge, 2020;
- Blitz, David. "Herbert Spencer: Philosophy of Evolution." In *Emergent Evolution: Qualitative Novelty and the Levels of Reality*, 24-34. Dordrecht: Springer Science, 1992.
- Boring, Edwin G. "The Beginning and Growth of Measurement in Psychology." *Isis*, 52;2(1961):238-257.
- Boring, Edwin G. A History of Experimental Psychology. New York: D. Appleton-Century Company, 1929.
- Bowler, Peter J. *Evolution: The History of an Idea*. Third Edition. Berkeley: University of California Press, 2003.

- Brain, Robert M., Cohen, Robert S. and Ole Knudsen (eds.). Hans Christian Ørsted and the Romantic Legacy in Science: Ideas, Disciplines, Practices. Boston Studies in the Philosophy of Science, Vol. 241. Dordrecht, The Netherlands: Springer, 2007.
- Brazier, Mary A. B. *A History of Neurophysiology in the 19th Century*. New York: Raven Press, 1987.
- Brock, Adrian. "History of the History of Psychology." In Oxford Research Encyclopedia of Psychology. Oxford University Press, 2020, https://oxfordrecom.proxy.library.upenn.edu/psychology/view/10.1093/acrefore/9780190236557.001.00 01/acrefore-9780190236557-e-464.
- Brown, Richard E. "The Life and Work of Donald Olding Hebb: Canada's Greatest Psychologist." *Proceedings of the Nova Scotian Institute of Science*, 44;1(2007):1-25.
- Brown, Richard E., and Peter M. Milner. "The Legacy of Donald O. Hebb: More than the Hebb Synapse." *Nature Reviews Neuroscience*, 4(2003):1013-1019.
- Burns, Alistair. "Another Nail in the Coffin of the Cognitive Paradigm of Dementia." *The British Journal of Psychiatry*, 194(2009):199-200.
- Cahan, David. "Helmholtz and the British Scientific Elite: From Force Conservation to Energy Conservation." *The Notes and Records of the Royal Society*, 66(2012):55-68.

Cahan, David. Helmholtz: A Life in Science. Chicago: The University of Chicago Press, 2018.

- Caneva, Kenneth L. "Ampère, the Etherians, and the Oersted Connexion." *The British Journal for the History of Science*, 13;2(1980):121-138.
- Cannon, Dorothy F. *Explorer of the Human Brain: The Life of Santiago Ramón y Cajal (1852-1934)*. New York: Henry Shuman, 1949.

- Cantor, Geoffrey. *Michael Faraday: Sandemanian and Scientist: A Study of Science and Religion in the Nineteenth Century*. London: MacMillan, 1991.
- Capshew, James H. "A History of Psychology Since 1945: A North American Review." In *A Historiography of the Modern Social Sciences*. Edited by Roger E. Backhouse and Philippe Fontaine, 144-182. New York: Cambridge University Press, 2014.
- Chasin, Gerald. "George Herbert Mead: Social Psychologist of the Moral Society." *Berkeley Journal of Sociology*, 9(1964):95-117.
- Christensen, Dan Ch. Hans Christian Ørsted: Reading Nature's Mind. Oxford: Oxford University Press, 2013.
- Clarke, Edwin, and L.S. Jacyna. *Nineteenth-Century Origins of Neuroscientific Concepts*. Berkeley: University of California Press, 1987.
- Cohen, Lawrence. *No Aging in India: Alzheimer's, the Bad Family, and Other Modern Things.* Berkeley, University of California Press, 1998.
- Coon, Deborah. "'One Moment in the World's Salvation.' Anarchism and the Radicalizing of William James." *The Journal of American History*, 83;1(1996):70-99.
- Cranefield, Paul F. "Carl Ludwig and Emil du Bois-Reymond A Study in Contrasts." Gesnerus: Swiss Journal of the History of Medicine and Sciences, 45(1988):271-282.
- Cranefield, Paul F. "Charles E. Morgan's 'Electro-Physiology and Therapeutics': An Unknown English Version of Du Bois-Reymond's 'Thierische Elektricität'. *Bulletin of the History of Medicine*, 31;2(1957):172-181.
- Cunningham, Andrew and Nicolas Jardine (eds.). *Romanticism and the Sciences*. Cambridge: Cambridge University Press, 1990.

- De Pierris, Graciela, and Michael Friedman. "Kant and Hume on Causality." In *The Stanford Encyclopedia of Philosophy*. Winter 2018 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/archives/win2018/entries/kant-hume-causality/.
- Degnen, Cathrine. "Ethnographies of Ageing." In *Routledge Handbook of Cultural Gerontology*. Edited by Julia Trigg and Wendy Martin, 115-112. New York: Routledge, 2015.
- Dettelbach, Michael. "Alexander von Humboldt Between Enlightenment and Romanticism." *Northeastern Naturalist*, 8;1(2001):9-20.
- Dewsbury, Donald A. "The Chicago Five: A Family Group of Integrative Psychobiologists." *History of Psychology*, 5;1(2002):16-37.
- Dolan, Brian. "Representing Novelty: Charles Babbage, Charles Lyell, and Experiments in Early Victorian Geology." *History of Science*, 36;3(1998):299-327.
- Dumit, Joseph. *Picturing Personhood. Brain Scans and Biomedical Identity*. Princeton: Princeton University Press, 2004.
- Eccles, J. C., and W. C. Gibson. *Sherrington: His Life and Thought*. New York: Springer International, 1979.
- Edwards, Paul N. *The Closed World: Computers and the Politics of Discourse in Cold War America*. Cambridge MA: The MIT Press, 1996.
- Engstrom, Stephen. "Knowledge and its Object." In *Kant's Critique of Pure Reason: A Critical Guide*. Edited by James R. O'Shea, 28-45. Cambridge: Cambridge University Press, 2017.
- Fearing, Franklin. "Marshall Hall." In *Reflex Action: A Study in the History of Physiological Psychology*, 122-145. Cambridge, MA: The MIT Press, 1970.

- Fenn, Wallace O. "Alexander Forbes 1882-1965: A Biographical Memoir." *Biographical Memoirs*, Vol. 40, 113-141. Washington, DC: National Academy of Sciences, 1969.
- Fierro, Catriel et al. "Science and Technology Studies and the Historiography of Psychology: Towards a Critical Analysis." *Trends in Psychology*, 27;4(2019):943-959.
- Finger, S. Minds Behind the Brain: A History of the Pioneers and Their Discoveries. Oxford: Oxford University Press, 2004.
- Finger, Stanley. Origins of Neuroscience: A History of Explorations into Brain Function. New York: Oxford University Press, 2001.
- Finkelstein, Gabriel. "Conquerors of the Künlün"? The Schlagintweit Mission to High Asia, 1854-1857." *History of Science*, 38(2000):179-218.
- Finkelstein, Gabriel. "M. du Bois-Reymond Goes to Paris." *The British Journal for the History* of Science, 36;3(2003):261-300.
- Finkelstein, Gabriel. *Emil du Bois-Reymond: Neuroscience, Self, and Society in Nineteenth-Century Germany.* Cambridge, MA: The MIT Press, 2013.
- Forman, Paul. "Weimar Culture, Causality, and Quantum Theory, 1918-1927: Adaptation by German Physicists and Mathematicians to a Hostile Intellectual Environment." *Historical Studies in the Physical Sciences*, 3(1971):1-115.
- Forster, Michael. "Hegel's Dialectical Method." In *The Cambridge Companion to Hegel*. Edited by Frederick C. Beiser, 130-170. Cambridge: Cambridge University Press, 1993.

Friedman, Michael. "Laws of Nature and Causal Necessity." Kant-Studien, 105(2014):531-553.

Galison, Peter. "The Ontology of the Enemy: Norbert Wiener and the Cybernetic Vision." *Critical Inquiry*, 21;1(1994):228-266.

- Garson, Justin. "The Birth of Information in the Brain: Edgar Adrian and the Vacuum Tube." *Science in Context*, 28;1(2015):31-52.
- Garson, Justin. "The Introduction of Information into Neurobiology." *Philosophy of Science*, 70;5(2003): 926-936.
- Geison, Gerald. *Michael Foster and the Cambridge School of Physiology*. Cambridge: Cambridge University Press, 1978.
- Gigerenzer, Gerd, and David J. Murray. *Cognition as Intuitive Statistics*. Hillsdale, NJ: Erlbaum, 1987.
- Gleick, James. *The Information: A History, a Theory, a Flood*. New York: Pantheon Books, 2011.
- Goffman, Erving. *Stigma: Notes on the Management of a Spoiled Identity*. New York: Simon and Schuster, 1963.
- Granit, R. Charles Scott Sherrington: An Appraisal. Garden City, NY: Doubleday, 1967.
- Grogan, Jessica. Encountering America: Humanistic Psychology, Sixties Culture & the Shaping of the Modern Self. New York: Harper Perennial, 2013.
- Guyer, Paul. "Introduction: The Starry Heavens and the Moral Law." In *The Cambridge Companion to Kant and Modern Philosophy*. Edited by Paul Guyer, 1-27. Cambridge:
 Cambridge University Press, 2006.
- Guyer, Paul. "Kant's Intellectual Development: 1746-1781." In *The Cambridge Companion to Kant*. Edited by Paul Guyer, 26-61. Cambridge: Cambridge University Press, 1992.

Hacking, Ian. "Canguilhem Amid the Cyborgs." Economy and Society, 27;2-3(1998):202-216.

Hacking, Ian. Mad Travelers: Reflections on the Reality of Transient Mental Illnesses.

University of Virginia Press, 1998.

Hacking, Ian. The Taming of Chance. Cambridge: Cambridge University Press, 1990.

Haeusermann, Tobias. "Caring Communities." *The Postgraduate Journal of Medical Humanities*, 2(2015):61-83.

- Hanna, Robert. "Completing the Picture of Kant's Metaphysics of Judgment." In The Stanford Encyclopedia of Philosophy. Winter 2018 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/entries/kant-judgment/supplement5.html.
- Hanna, Robert. "Kant's Theory of Judgment." In The Stanford Encyclopedia of Philosophy.
 Winter 2018 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/entries/kant-judgment/index.html.
- Haraway, Donna. "A Cyborg Manifesto: Science, Technology, and Socialist-Feminism in the Late Twentieth Century." In Simians, Cyborgs and Women: The Reinvention of Nature, 149-181. New York: Routledge, 1991.
- Haraway, Donna. "Situated Knowledges: The Science Question in Feminism and the Privilege of Partial Perspective." *Feminist Studies*, 14;3(1988):575-599.
- Haraway, Donna. "The Biological Enterprise: Sex, Mind, and Profit from Human Engineering to Sociobiology." In Simians, Cyborgs and Women: The Reinvention of Nature, 43-68. New York: Routledge, 1991.
- Harrington, Anne. "The Brain and the Behavioral Sciences." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences*. Edited by Peter J. Bowler and John V. Pickstone, 504-532. Cambridge: Cambridge University Press, 2009.
- Harrington, Anne. *Medicine, Mind and the Double Brain*. Princeton: Princeton University Press, 1987.

- Healy, David. *The Creation of Psychopharmacology*. Cambridge, MA: Harvard University Press, 2002.
- Heims, Steve J. John von Neumann and Norbert Wiener: From Mathematics to the Technologies of Life and Death. Cambridge, MA: The MIT Press, 1980.
- Heims, Steve J. *The Cybernetics Group: Constructing a Social Science for Post-War America*. Cambridge, MA: The MIT Press, 1991.
- Heinämaa, Sara. "Phenomenological Responses to Gestalt Psychology." In *Psychology and Philosophy: Inquiries into the Soul from Late Scholasticism to Contemporary Thought. Studies in the History of Philosophy of Mind*, Vol 8. Edited by Sara Heinämaa and Martina Reuter, 263-284. Dordrecht: Springer, 2009.
- Herman, Ellen. "The Dilemmas of Democratic Morale." In *The Romance of American Psychology: Political Culture in the Age Of Experts*, 49-82. Berkeley: University of California Press, 1995.
- Hodgkin, A. L. "Edgar Douglas Adrian, Baron Adrian of Cambridge, 30 November 1889 4 August 1977." *Biographical Memoirs of Fellows of the Royal Society*, 25(1979):1-73.
- Horan, Caley Dawn. Actuarial Age: Insurance and the Emergence of Neoliberalism in the Postwar United States. A dissertation submitted to the faculty of the graduate school of the University of Minnesota, 2011.
- Hunt, Bruce J. Pursuing Power and Light: Technology and Physics from James Watt to Albert Einstein. Baltimore, MD: The Johns Hopkins University Press, 2010.
- Huxley, A. F. "Kenneth Stewart Cole." *Biographical Memoirs*, Vol. 70, 24-46. Washington, DC: The National Academies Press, 1996.

Hydén, Lars-Christer. Entangled Narratives: Collaborative Storytelling and the Re-Imagining of Dementia. Oxford: Oxford University Press, 2017.

J. R. P. "Prof. Walter Nernst, For. Mem. R.S." Nature, 149;3779(1942):375-376.

- Jacyna, Stephen L. "Process and Progress: John Hughlings Jackson's Philosophy of Science." *Brain*, 134(2011):3121-3126.
- Jolley, Nicholas (ed.). *The Cambridge Companion to Leibniz*. Cambridge: Cambridge University Press, 1995.
- Jones, Edward G. "Santiago Ramón y Cajal and the Croonian Lecture, March 1894." *TINS*, 17;5(1994):190-192.
- Jungnickel, Christa and Russell McCormmach. "Establishing Physics at the Universities." In *The Second Physicist: On the History of Theoretical Physics in Germany*. Archimedes: New Studies in the History and Philosophy of Science and Technology, Vol. 48. Edited by Jed Z. Buchwald, 51-72. Switzerland: Springer, 2017.
- Kay, Lily E. "From Logical Neurons to Poetic Embodiments of Mind: Warren S. McCulloch's Project in Neuroscience." *Science in Context*, 14;4(2001):591-614.
- Kay, Lily E. The Molecular Vision of Life: Caltech, the Rockefeller Foundation, and the Rise of the New Biology. New York: Oxford University Press, 1993.
- Keuck, Lara. "Slicing the Cortex to Study Mental Illness: Alois Alzheimer's Pictures of Equivalence." In *Vital Models: The Making and Use of Models in the Brain Sciences*. Edited by Tara Mahfoud, Sam McLean, and Nikolas Rose, 25-51. Cambridge, MA: Elsevier, 2017.

- Kremer, Richard L. "Physiology." In *The Cambridge History of Science, Vol. 6: The Modern Biological and Earth Sciences*. Edited by Peter J. Bowler and John V. Pickstone, 342-366. Cambridge: Cambridge University Press, 2009.
- Kuhn, Thomas. *The Structure of Scientific Revolutions*. Chicago: The University of Chicago Press, 1970.
- Leibing, Annette, and Lawrence Cohen (eds.). *Thinking about Dementia: Culture, Loss, and the Anthropology of Senility.* New Brunswick: Rutgers University Press, 2006.
- Lenoir, Timothy. "Models and Instruments in the Development of Electrophysiology, 1845-1912." *Historical Studies in the Physical and Biological Sciences*, 17;1(1986):1-54.
- Liddell, Edward George Tandy. "Charles Scott Sherrington 1857-1952." *Biographical Memoirs* of Fellows of the Royal Society, 8;12(1952):241-270.
- Limnatis, Nectarios G. *German Idealism and the Problem of Knowledge: Kant, Fichte, Schelling, and Hegel.* Studies in German Idealism, Vol. 8. Edited by Reinier Munk. Springer: 2008.
- Lykknes, Annette, Opitz, Donald L., and Brigitte Van Tiggelen (eds.). For Better or For Worse? Collaborative Couples in the Sciences. Science Networks Historical Studies, Vol. 44. New York: Springer, 2012.

Mackenzie, Catriona and Natalie Stoljar. "Introduction: Autonomy Refigured." In *Relational Autonomy: Feminist Perspectives on Autonomy, Agency, and the Social Self.* Edited by Catriona Mackenzie and Natalie Stoljar, 3-31. New York: Oxford University Press, 2000.
MacKenzie, Donald. "Eugenics in Britain." *Social Studies of Science*, 6(1976):499-532.

- Mandler, George. "The Birth of Modern Psychology: Wilhelm Wundt and William James." In A History of Modern Experimental Psychology: From James and Wundt to Cognitive Science, 51-75. Cambridge, MA: The MIT Press, 2007.
- Mandler, Jean Matter, and George Mandler. "The Diaspora of Experimental Psychology: The Gestaltists and Others." In *Perspectives in American History*, Vol. 2, 371-419.
 Cambridge, MA: Charles Warren Center for Studies in American History, Harvard University, 1968.
- Maybee, Julie E., "Hegel's Dialectics." In *The Stanford Encyclopedia of Philosophy*. Winter 2016 Edition. Edited by Edward N. Zalta, https://plato.stanford.edu/entries/hegel-dialectics.
- Mazzarello, Paolo. *Golgi: A Biography of the Founder of Modern Neuroscience*. New York: Oxford University Press, 2010.
- McIlwain, Henry. "Neurochemistry and Sherrington's Enchanted Loom." *Journal of the Royal Society of Medicine*, 77(1984):417-425.
- McLaughlin, Brian P. "The Connectionism/Classicism Battle to Win Souls." *Philosophical Studies: An International Journal for Philosophy in the Analytic Tradition*, 71;2(1993):163-190.
- Meulders, Michel. *Helmholtz: From Enlightenment to Neuroscience*. Translated and edited by Laurence Garey. Cambridge, MA: The MIT Press, 2010.

Milner, Peter M. "The Cell Assembly: Mark II." Psychological Review, 64;4(1957):242-252.

Milner, Peter M. "The Mind and Donald O. Hebb." Scientific American, 268;1(1993):124-129.

- Möller, P. L. "The Life of H. C. Oersted." In *The Soul in Nature, with Supplementary Contributions*. By Hans Christian Oersted, translated by Leonora and Joanna B. Horner, vii-xxii. London: Dawsons of Pall Mall, 1966.
- Morgan, S. R. "Schelling and the Origins of his *Naturphilosophie*." In *Romanticism and the Sciences*. Edited by Andrew Cunningham and Nicholas Jardine, 25-37. Cambridge:
 Cambridge University Press, 1990.

Morus, Iwan Rhys. Michael Faraday and the Electrical Century. Cambridge: Icon Books, 2004.

- Moser, Ingunn. "Dementia and the Limits to Life: Anthropological Sensibilities, STS Interferences, and Possibilities for Action in Care." *Science, Technology, & Human Values*, 36;5(2011):704-722.
- Moxley, Roy A. "Some Early Similarities and Later Differences Between Bertrand Russell and B. F. Skinner." *The Behavior Analyst*, 26(2003):111-130.
- Musolf, Gil Richard. "William James and Symbolic Interactionists." *Sociological Focus*, 27;4(1994):303-314.
- Nersessian, Nancy J. Faraday to Einstein: Constructing Meaning in Scientific Theories. Dordrecht: Martinus Nijhoff Publishers, 1984.
- Nicoll, Roger A. "A Brief History of Long-Term Potentiation." Neuron, 93(2017):281-290.
- O'Donnell, John M. *The Origins of Behaviorism: American Psychology, 1870-1920.* New York: New York University Press, 1985.

Ogilvie, Marilyn, and Joy Harvey (eds.). *The Biographical Dictionary of Women in Science: Pioneering Lives from Ancient Times to the Mid-20th Century, Vol. 2, L-Z.* New York: Routledge, 2000.

- Olby, Robert. *The Path to the Double Helix: The Discovery of DNA*. Seattle: University of Washington Press, 1974.
- Pearce, Trevor. "The Origins and Development of the Idea of Organism-Environment Interaction." In *Entangled Life: History, Philosophy and Theory of the Life Sciences*.
 Edited by G. Barker et al., 13-32. Dordrecht: Springer Science, 2014.
- Pickering, Andrew. *The Cybernetic Brain: Sketches of Another Future*. Chicago: University of Chicago Press, 2010.
- Pinkard, Terry. *German Philosophy 1760-1860: The Legacy of Idealism*. Cambridge: Cambridge University Press, 2002.
- Porter, Dorothy. *Health Citizenship: Essays in Social Medicine and Biomedical Politics*. Berkeley: University of California Medical Humanities Press, 2011.
- Porter, Roy. A Social History of Madness: Stories of the Insane. London: Orion Books, 1996.

Porter, Roy. Madness: A Brief History. New York: Oxford University Press, 2002.

- Porter, Roy. *The Cambridge Illustrated History of Medicine*. Cambridge: Cambridge University Press, 2001.
- Porter, Theodore M. *The Rise of Statistical Thinking: 1820-1900*. Princeton: Princeton University Press, 1986.
- Porter, Theodore M. *Trust in Numbers: The Pursuit of Objectivity in Science and Public Life.* Princeton: Princeton University Press, 1995.
- Porter, Theodore M., and Dorothy Ross (eds.). *The Cambridge History of Science, Vol. 7. The Modern Social Sciences.* Cambridge: Cambridge University Press, 2003.
- Purrington, Robert D. *Physics in the Nineteenth Century*. New Brunswick: Rutgers University Press, 1999.

- Rajan, Tilottama. "The Vitality of Idealism: Life and Evolution in Schelling's and Hegel's Systems." In *Marking Time: Romanticism and Evolution*. Edited by Joel Faflak, 239-269. Toronto: University of Toronto Press, 2017.
- Ramirez-Bermudez, Jesus. "Alzheimer's Disease: Critical Notes on the History of a Medical Concept." *Archives of Medical Research*, 43(2012):595-599.
- Richards, Robert J. "Did Goethe and Schelling Endorse Species Evolution?" In *Marking Time: Romanticism and Evolution*. Edited by Joel Faflak, 219-238. Toronto: University of Toronto Press, 2017.
- Richards, Robert J. *The Romantic Conception of Life: Science and Philosophy in the Age of Goethe*. Chicago: The University of Chicago Press, 2002.
- Riskin, Jessica. The Restless Clock: A History of The Centuries-Long Argument Over What Makes Living Things Tick. Chicago: University of Chicago Press, 2016.
- Robbins, Jessica. "Expanding Personhood Beyond Remembered Selves: The Sociality of Memory at an Alzheimer's Center in Poland." *Medical Anthropology Quarterly*, (2019):1-18.
- Rose, Nikolas, and Joelle Abi-Rached. "Governing Through the Brain: Neuropolitics, Neuroscience and Subjectivity." *The Cambridge Journal of Anthropology*, 32;1(2014):3-23.
- Rose, Nikolas. "Assembling the Modern Self." In *Rewriting the Self: Histories from the Renaissance to the Present*. Edited by Roy Porter, 224-248. London: Routledge, 1997.
- Rose, Nikolas. *Inventing Our Selves: Psychology, Power and Personhood*. Cambridge: Cambridge University Press, 1996.

- Rose, Nikolas. *The Politics of Life Itself: Biomedicine, Power, and Subjectivity in the 21st Century.* Princeton: Princeton University Press, 2006.
- Roth, Michael, S. "Remembering Forgetting: Maladies de la Memoire in Nineteenth-Century France." *Representations, Special Issue: Memory and Counter-Memory*, (1989):49-68.
- Rudwick, Martin J. S. *Earth's Deep History: How it Was Discovered and Why it Matters.* Chicago: The University of Chicago Press, 2014.
- Schaffer, Simon. "The Phoenix of Nature: Fire and Evolutionary Cosmology in Wright and Kant." *Journal for the History of Astronomy*, x(1978): 180-200.
- Schmidgen, Henning. "Leviathan and the Myograph: Hermann Helmholtz's 'Second Note' on the Propagation Speed of Nervous Stimulations." *Science in Context*, 28;3(2015):357-396.
- Schmidgen, Henning. *The Helmholtz Curves: Tracing Lost Time*. Translated by Nils F. Schott. New York: Fordham University Press, 2014.
- Schönfeld, Martin, and Thompson, Michael, "Kant's Philosophical Development." In *The Stanford Encyclopedia of Philosophy*. Winter 2019 Edition. Edward N.

Zalta, https://plato.stanford.edu/archives/win2019/entries/kant-development/.

- Schuetze, S. M. "The Discovery of the Action Potential." *Trends in Neuroscience*, 6(1983):164-168.
- Sejnowski, Terrence J. "The Book of Hebb." Neuron, 24(1999):773-776.
- Seyfarth, Ernst-August. "Julius Bernstein (1839-1917): Pioneer Neurobiologist and Biophysicist." *Biological Cybernetics*, 94(2006):2-8.
- Shepherd, Gordon M. Creating Modern Neuroscience: The Revolutionary 1950s. New York: Oxford University Press, 2010.

- Sherrington, Charles S. *Goethe on Nature and on Science*. Cambridge: Cambridge University Press, 1942.
- Sherrington, Charles S. *The Endeavour of Jean Fernel*. Cambridge: Cambridge University Press, 1946.
- Shorter, Edward. *Before Prozac: The Troubled History of Mood Disorders in Psychiatry*. New York: Oxford University Press, 2009.
- Smith, Crosbie, and M. Norton Wise. *Energy and Empire: A Biographical Study of Lord Kelvin*. Cambridge University Press, 1989.
- Smith, Crosbie. The Science of Energy: A Cultural History of Energy Physics in Victorian Britain. The University of Chicago Press, 1998.
- Smith, Roger. *Between Mind and Nature: A History of Psychology*. London: Reaktion Books, 2013.
- Smith, Roger. *Inhibition: History and Meaning in the Sciences of Mind and Brain*. Berkeley: University of California Press, 1992.

Smith, Roger. The Fontana History of the Human Sciences. London: Fontana Press, 1997.

- Sokal, Michael M. "The Gestalt Psychologists in Behaviorist America." *The American Historical Review*, 89;5(1984):1240-1263.
- Stahnisch, F. W. "From 'Nerve Fiber Regeneration' to 'Functional Changes' in the Human
 Brain—On the Paradigm-Shifting Work of the Experimental Physiologist Albrecht Bethe (1872-1954) in Frankfurt am Main." *Frontiers in Systems Neuroscience*, 10;6(2016):1-16.
- Sulloway, Frank J. *Freud, Biologist of the Mind: Beyond the Psychoanalytic Legend.* Cambridge, MA: Harvard University Press, 1992.

- Swazey, Judith P. "Sherrington's Concept of Integrative Action." *Journal of the History of Biology*, 1;1(1968):57-89.
- Temkin, Owsei. *The Double Face of Janus and Other Essays in the History of Medicine*. Baltimore: Johns Hopkins University Press, 2006.

Toulmin, Stephen, and June Goodfield. The Discovery of Time. New York: Harper & Row, 1965.

- Travers, T. H. E. "Samuel Smiles and the Origins of 'Self-Help': Reform and the New Enlightenment." *Albion: A Quarterly Journal Concerned with British Studies*, 9;2(1977):161-187.
- Tresch, John. *The Romantic Machine: Utopian Science and Technology after Napoleon*. Chicago: The University of Chicago Press, 2012.
- Turkel, William J. "Discovering Electric Worlds." In Spark from the Deep: How Shocking Experiments with Strongly Electric Fish Powered Scientific Discovery, 178-205.
 Baltimore: Johns Hopkins University Press, 2013.
- Turkle, Sherry. *The Second Self: Computers and the Human Spirit,* Twentieth Anniversary Edition. Cambridge, MA: The MIT Press, 2005.
- Turner, Fred. *The Democratic Surround: Multimedia and American Liberalism from World War II to the Psychedelic Sixties.* Chicago: The University of Chicago Press, 2013.
- Valenstein, Eliot S. The War of the Soups and the Sparks: The Discovery of Neurotransmitters and the Dispute Over How Nerves Communicate. New York: Columbia University Press, 2006.
- Vaughan, Michael. "Introduction: Henri Bergson's Creative Evolution." *SubStance*, 36;3(2007)7-24.
- Walshe, F. M. R. "Reviews: A Foundation of Neurology." British Medical Journal, (1947):823.

- Watkins, Eric. "Kant on the Distinction Between Sensibility and Understanding." In *Kant's Critique of Pure Reason: A Critical Guide*. Edited by James R. O'Shea, 9-27.
 Cambridge: Cambridge University Press, 2017.
- Watkins, Eric. *Kant and the Metaphysics of Causality*, Cambridge: Cambridge University Press, 2005.
- Watrin, João Paulo. "The Ambiguous "New History of Psychology": New Questions for Brock (2017)." *History of Psychology*, 20;2(2017):225-237.
- Weidman, Nadine M. Constructing Scientific Psychology: Karl Lashley's Mind-Brain Debates. Cambridge: Cambridge University Press, 1999.
- Wellmann, Janina. *The Form of Becoming: Embryology and the Epistemology of Rhythm*, 1760-1830. Cambridge, MA: MIT Press, 2017.
- Westphal, Kenneth R. "Kant's Dynamical Principles: The Analogies of Experience." In *Kant's Critique of Pure Reason: A Critical Guide*. Edited by James R. O'Shea, 184-204.
 Cambridge: Cambridge University Press, 2017.
- Wetzels, Walter D. "Johann Wilhelm Ritter: Romantic Physics in Germany." In *Romanticism* and the Sciences. Edited by Andrew Cunningham and Nicholas Jardine, 199-212.
 Cambridge: Cambridge University Press, 1990.

Williams, L. Pearce. Michael Faraday: A Biography. New York: Basic Books, 1965.

Wise, M. Norton. Aesthetics, Industry, and Science: Hermann von Helmholtz and the Berlin Physical Society. Chicago: The University of Chicago Press, 2018.

York, George K. and David A. Steinberg. "Hughlings Jackson's Neurological Ideas." *Brain*, 134(2011):3106-3113.

- Young, Robert Maxwell. *Mind, Brain and Adaptation in the Nineteenth Century*. New York: Oxford University Press, 1970.
- Zammito, John. "Reconstructing German Idealism and Romanticism: Historicism and Presentism." *Modern Intellectual History*, 1;3(2004):427-438.

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