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The Birth of Information in the Brain: Edgar Adrian and the Vacuum Tube

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Abstract: As historian Henning Schmidgen notes, the scientific study of the nervous system would have been ‘unthinkable’ without the industrialization of communication in the 1830s. Historians have investigated extensively the way nerve physiologists have borrowed concepts and tools from the field of communications, particularly regarding the nineteenth-century work of figures like Helmholtz and in the American Cold War Era. The following focuses specifically on the interwar research of the Cambridge physiologist Edgar Douglas Adrian, and on the technology that led to his Nobel-Prize-winning research, the thermionic vacuum tube. Many countries used the vacuum tube during the war for the purpose of amplifying and intercepting coded messages. These events provided a context for Adrian’s evolving understanding of the nerve fiber in the 1920s. In particular, they provide the background for Adrian’s transition around 1926 to describing the nerve impulse in terms of “information,” “messages,” “signals,” or even “codes,” and for translating the basic principles of the nerve, such as the all-or-none principle and adaptation, into such an “informational” context. The following also places Adrian’s research in the broader context of the changing relationship between science and technology, and between physics and physiology, in the first few decades of the twentieth century.

1. Introduction.

On November 3, 1925, the English nerve physiologist Edgar Douglas Adrian of Trinity College, Cambridge, and his research assistant Yngve Zotterman, discovered “a great secret of life” (Zotterman 1969, 220). Adrian and Zotterman had been working on a frog’s sensory nerve and muscle. They had impaled the nerve with electrodes and stretched the muscle. A vacuum tube amplified information about the impulse and routed it into a capillary electrometer, which projected it onto a photographic screen. It appeared there as a series of erratic waves. Earlier, Zotterman had suggested a method for observing the action potential of a single sensory neuron, a technical feat that had yet to be accomplished. The two men were able to do this by removing small strips from the muscle in which the nerve was embedded, so that fewer and fewer neurons in the nerve were active. As they did this, the erratic wave on the photographic plate became gradually simplified until it formed a wave with a simple, regular, frequency and amplitude, “like a beating heart.”[1] This was the coveted representation of a single neuron’s activity. During the procedure, Adrian scrambled back and forth between the lab and the photographic darkroom to ensure that this momentous event was recorded for posterity (Zotterman 1969, 220; Adrian and Zotterman 1926).

This event had thoroughgoing epistemic significance for nerve physiology, in at least two respects. Firstly, it changed the way nerve scientists posed questions about the nervous system. Before this event, questions about the activity of a single sensory neuron could

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[1] Adrian to Forbes in a letter dated November 19, 1925 (Alexander Forbes papers, Box 1, Folder 2).

only be approached "indirectly," by complex and controversial inferences from other sources of data. For example, one question that Adrian was preoccupied with was whether the all-or-none principle was true of sensory *and* motor neurons, or merely of motor neurons (Adrian and Forbes 1922, 302). Another question had to do with the nature of decrement in narcoticized nerve (Adrian 1913; also see Frank 1994). As a consequence of Adrian's work, these questions could now be posed "directly;" they could be asked, as it were, of the "neuron itself." With various collaborators, Adrian devoted the next several years to using these sorts of direct recordings in the attempt to demonstrate that the basic principles of nerve activity – the all-or-none principle and adaptation – were universal across different types of nerves and in different biological species.[2]

In addition to changing the way that nerve physiologists posed questions, however, their study changed the *kinds* of questions that physiologists could pose. Shortly after his discovery, Adrian began describing the nerve as carrying "information" to the brain about the outside world. In Adrian's writings, the electrical disturbances that traversed the sensory neuron were even transformed into *messages*, *signals*, and *codes* (Adrian 1928, 14; Adrian 1932, 12; Adrian and Bronk 1929a, 145). These terms only became more prominent in his writing after his popularization of the electroencephalogram in the mid-1930s and the associated notion of 'brain-writing' which quickly entered into popular discourse (Borck 2005; 2008a; 2008b).

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[2] See, e.g., Adrian (1926; 1926a); Adrian and Zotterman (1926a; 1926b); Adrian and Matthews (1927; 1927a; 1928; Adrian and Bronk (1928, 1929; 1929a).

This transition is notable, as the term “information,” and its cognates such as “message” and “signal,” had been almost entirely absent from Adrian's work prior to 1926. Likewise these terms were not used with any appreciable frequency in the work of Adrian’s colleagues and interlocutors prior to the 1930s. Terms such as “message,” “signal,” and “information,” are absent, for example, in Sherrington’s *The Integrative Action of the Nervous System* of 1906; they are absent from the writings of Herbert Gasser prior to the 1930s; they are absent from the work of Alan Hodgkin, with a single exception in the late 1930s which describes the nerve impulse as a “message” (Hodgkin and Huxley 1939, 710). The term “message” occurs very sparingly in the work of Alexander Forbes (see Forbes 1922a, 361; Forbes et al. 1926, 307). With rare exceptions, physiologists described nerve activity using the stark, colorless language of “impulses,” “disturbances,” “reactions,” and “activity.” By the mid-1920s, however, physiologists like Adrian could begin considering *how* precisely a neuron transmitted information to the brain about changes in the intensity of the stimulus. For example, they could ask whether it did so merely by modulating its frequency or by some other means (see Adrian 1931, 21). In short, by using the language of information, nerve physiologists like Adrian posed questions that could not be asked previously, namely, questions about the abstract relationship between impulse and stimulus.

One could pursue many different trails here regarding Adrian's shift towards this “informational” language but three are of particular value for the way in which they demonstrate this transition. Firstly, few historians have considered the significance of Adrian's work for the historiography of information in the life sciences. While many historians have explored the complex interrelationship between communications technology and nerve physiology in the nineteenth-century and during the Cold War Era, the interwar period has been largely neglected. Exploring the relation between nerve physiology and communications during this time can also help us to appreciate the changes that the very ideas of *information* and *communication* were undergoing in that period. This essay begins that process by focusing on the early-twentieth-century research of Adrian, and the apparatus that transformed his laboratory practice and understanding of neurons, the thermionic vacuum tube. It relies on published primary sources and archival material, including Adrian's correspondence with the Harvard physiologist Alexander Forbes.

There was, however, a dramatic political and technological context underlying this "informational" shift in Adrian's work. The vacuum tube initially came into wide use as an amplifier and detector of radio signals during World War I; many figures in many countries used the vacuum tube for the purpose of military communications. During the war, Forbes suspended his work at Harvard physiological laboratory and volunteered as a radio engineer for the American Navy. He thereby gained facility in the use of vacuum tube, and when the war ended he convinced Adrian of its value for the study of nerves. Because of its role in communications technology, and particularly because of its well-known wartime applications, the vacuum tube came already embedded in a rich matrix of practices for the manipulation and detection of information, specifically coded messages. The vacuum tube, in Adrian's hands, "carried the memory" of these practices along with it.

Adrian's work, thirdly, was instrumental in shaping the context of broader changes that nerve physiology as a whole was undergoing. In the first few decades of the twentieth century, nerve physiology witnessed a pronounced shift of emphasis onto technological innovation, much of it spawned by the need for manipulating and recording the electrical activity of nerves. This renewed emphasis on technology went hand-in-hand with a disciplinary reorientation of physiology, in which physiologists increasingly turned to physics, mathematics, and electrical engineering, to articulate their research questions and to generate and analyze laboratory data. Yet at the same time, and without any perceived contradiction, the nervous system underwent a kind of *etherealization* or sublimation. The material principles of nerve transmission, such as the all-or-none principle and adaptation, were systematically retranslated into informational and even teleological terms. The all-or-none principle became something like a constraint on the *syntax* by which information could be transmitted to the brain. The adaptation of the sensory nerve to a constant stimulus became a teleological principle of economy for reducing unnecessary or repetitive messages. The basic principles of the nerve impulse were no longer brute physical facts to be grasped by the scientist equipped with physical methods, but abstract correlations between patterns of stimuli and nerve response, ultimately to be dissolved into pure statistics. This is not to say that nobody before Adrian had construed the nerve impulse as a sort of “message.” One way to approach the distinctness of Adrian’s use of communication analogies is to contrast his use of such analogies with that of his predecessors and successors.

2. Communication and Coding Before and After Adrian.

For almost a century and a half, the brain sciences and nerve physiology have repeatedly looked to the field of communications to borrow its conceptual framework and technological means (Clarke and Jacyna 1987, especially Chapter 5; also see Kirkland 2002). The mid-nineteenth century German physiologists Hermann von Helmholtz and Emil du Bois-Reymond occasionally compared the nervous system to the electric telegraph network that traversed Germany; likewise, the popular press described electrical telegraphy as the 'nervous system' of the nation (Hunt 1994, 319; also see Hunt 2010, 84). A century later, the mid-twentieth-century American neurobiologist Warren McCulloch, amongst many others, relied on a quantitative measure of information that emerged from cybernetics and information theory.[3] At the same time, terms such as 'information', 'code', and 'message' penetrated even molecular genetics and ethology (Keller 1995; Sarkar 1996; Kay 2000).[4] As historian Henning Schmidgen has argued, the scientific practices underlying nerve physiology would have been 'unthinkable' without the industrialization of communication that began in the 1830s (Schmidgen 2009, 14). While historians have studied the use of communication analogies in the mid-nineteenth century work of Helmholtz and du Bois-Reymond (Lenoir 1994; Otis 2002), as well as those culled from information theory and cybernetics in mid-twentieth-century American neuroscience (e.g., Kay 2000; 2001; Heims 1991, especially Chapter 10; Brain 2002),

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[3] See MacKay and McCulloch 1952 for the first theoretical application of Shannon's (1948) information measure to neural transmission.

[4] The issue of parallels between the two fields deserves extensive independent treatment. For a recent technical overview of information in ethology, see Sarkar 2013.

few have examined the use of communication analogies in the interim, and particularly during the interwar period.

By placing Adrian's work in the context of the interplay between communications industry and nerve physiology, it is neither necessary to deny the specificity of Adrian's sense of "information" and cognate terms, nor to entirely absorb them into something like a "tradition" of physiology. Rather, it is sufficient to compare Adrian's usage through a contrast with that of both his predecessors and his successors. As will become clear, when Adrian posed the question of how much "information" the nervous system can extract from nerve "message," he did not mean the same thing by "information" that Helmholtz meant by the "Nachricht" carried by the nerve fibers. Nor did Adrian mean the same thing by "information" that later neuroscientists and information theorists such as Donald MacKay and Warren McCulloch meant by a neuron's "informational capacity" (e.g., Adrian 1928, 91; Helmholtz 1883, 873; MacKay and McCulloch 1952). Such comparative analysis provides an initial fix on Adrian's use and sheds light on the way that the very *concepts* of communication and information were changed during World War I.

Historian Timothy Lenoir has identified the mid-nineteenth-century work of German physiologists Helmholtz and du Bois-Reymond as a point of origin for studying the appropriation of themes from communications technology into the brain sciences (Lenoir 1994 but also see Kirkland 2002; Otis 2002; De Palma and Pareti 2007). By the end of the nineteenth-century, the British Empire had built an extensive international telegraph network to promote its system of colonial rule that controlled over one-fifth of the land mass of the earth. The telegraph was considered the very "nerves of empire" (Hunt 1994, 312-313; also see Hunt 2010, 85-93). In Helmholtz's Germany, the telegraph was a primary mechanism by which provincial news quickly reached the capital, and by which instructions could be sent, in return, to provincial authorities.

It is little surprising, then, that Helmholtz and du Bois-Reymond occasionally relied on this technological and political analogy to describe the nervous system itself. The nervous system, like the telegraph, carried "messages" (*Nachricht*, which can also be translated as "news"), and "dispatches," from the sensory periphery of the body to the brain, and, in turn, carried "commands" or "intentions" back outward. As Helmholtz wrote,

> *…so dürfen wir die Nervenfäden nicht unpassend mit den elektrischen Telegraphendrähten vergleichen, welche einmal augenblicklich jede* Nachricht *von den äussersten Grenzen her dem regierenden Centrum zuführen, und dann ebenso dessen* Willensmeinung *nach jedem einzelnen Theile des Ganzen zurückbringen…*[…we may not improperly compare the nerve fibres with the electric telegraph wires, which first immediately carry each *message* from the most distant parts to the ruling center, and then in the same way bring the *intention of its will* back to every single part of the whole…]" (Helmholtz, 1883, 873; emphasis mine).

Du Bois-Reymond – Helmholtz's colleague, friend, and fellow student of Johann Müller – used the same analogy and Helmholtz acknowledged his friend's chronological priority with it (De Palma and Pareti 2007, 108). In a speech delivered on February 22, 1851, du Bois-Reymond stated:

> *…so empfängt auch die Seele in ihrem Bureau, dem Gehirn, durch ihre Telegraphendrähte, die Nerven, unaufhörlich* Depeschen *von allen Grenzen ihres Reiches, des Körpers, und theilt nach allen Richtungen* Befehle *an ihre Beamten, die Muskeln, aus* […so the soul in its office, the brain, incessantly receives *dispatches* from all parts of its empire, the body, through the telegraph wires, the nerves, and dispenses *commands* in all directions to its officials, the muscles] (du Bois-Reyomond 1886, 51; emphasis mine).

Moreover, the telegraph analogy entered into popular descriptions of nerve activity as well. The English physician Spencer Thomson, in his *Dictionary of Domestic Medicine and Household Surgery* of 1852, for example, gave the following characterization under his entry for 'hunger': "To use a simile, the brain may be likened to a great central telegraph office, to which the wires – nerves – convey the information from all parts of the body that supplies are wanted…" (Thomson 1852, 285).

Of course, the significance of such analogies should not be exaggerated. Lenoir, for one, has suggested that Helmholtz considered the electrical impulses of the nerve as a "perceptual analogue of Morse code."[5] But this was not the way that Helmholtz described the nervous message. To describe the nerve as implementing a "code" is to attribute a specific, language-like structure to the nerve impulse itself. It is not *merely* to say that it carries news or commands, but that it does so *via* a systematic set of correspondences between nerve activity and the outer stimuli. But these were not the sorts of questions that Helmholtz and du Bois-Reymond were posing *of the nerve*. They were, however, the kinds of questions that Adrian and his successors posed, thanks to specific technologies that allowed them to interrogate the single neuron's activity.

Yet, furthermore, the very purpose of these analogies is in some doubt. It is not clear whether the main purpose of the telegraph analogy was to characterize the nervous system as a communication device. Some historians have suggested that the main purpose of the analogy was much more mundane (Boring 1950, 95; De Palma and Pareti 2007). It was to illustrate that in the nervous system, the same cause could have many effects. The electric telegraph was not merely a mechanism for carrying messages, it was also used for the transmission of impulses that could have a range of effects, from producing a message, ringing a bell, or defusing a mine, all depending on the terminal to which the impulse was connected. Likewise, in the nervous system, one and the same mechanism – electrical impulses carried by a nerve – had varying physiological effects depending on the kind of terminal to which it was attached. Helmholtz himself clarified one purpose for these analogies in the following passage:

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[5] Lenoir 1994, 186; also see Otis 2002, 118.

> *Man hat die Nerven vielfach nicht unpassend mit Telegraphendrähten verglichen. …Dennoch kann man, je nachdem man seine Enden mit verschiedenen Apparaten in Verbindung setzt, telegraphische Depeschen geben, Glocken läuten, Minen entzünden, Wasser zersetzen, Magnete bewegen, Eisen magnetisiren, Licht entwickeln u. s. w. Aehnlich in den Nerven…bringt er Bewegungen hervor, Absonderungen von Drüsen, Ab – und Zunahme der Blutmenge, der Röthe und der Wärme einzelner Organe, dann wieder Lichtempfindungen, Gehörempfindungen u. s. w.* [The nerves have often and not inappropriately been compared with telegraph wires…Nonetheless one can, depending on how one arranges the connections with various apparatuses, give telegraphic dispatches, ring bells, ignite mines, decompose water, move magnets, magnetize iron, develop light, and so on. So with the nerves…it brings forth movements, gland secretions, decrease and increase in the amount of blood, the redness and warmth of individual organs, then again light sensations, sensations of sound, and so on] (Helmholtz 1863, 222).

While acknowledging that the nervous system could convey ‘news’, ‘dispatches’, and ‘orders’, du Bois-Reymond had a similar purpose in using the analogy, namely, to illustrate certain physiological properties of nerves, such as, for example, that the brain does not know from what point of the nerve the painful feeling originates just as a telegraph station sending a message is unknown to the recipient at the final destination or that the ‘news’ passing through a wire remained hidden from external perspective (De Palma and Pareti 2007, 108.) Despite their use of analogies drawn from human communication, as well as their acknowledgement that the nervous system could carry "news," the role of these analogies cannot be identified in any simple manner with the role they came to play in Adrian's work or for that matter in those that came after in the Cold War Era.

Some historians have placed special emphasis on the use of information analogies in neuroscience in the wake of the cybernetics movement and information theory during, and in the immediate aftermath of, World War II (e.g., Kay 2000; 2001; Heims 1991, especially Chapter 10; Brain 2002). A representative work is MacKay and McCulloch (1952), and the work of their colleagues such as American logician Walter Pitts and cognitive science Jerome Lettvin.[6] In some ways, the concept of "information" in this tradition was quite antithetical to the ways that both Helmholtz and Adrian used the term.

The purpose of MacKay and McCulloch's work was to apply Claude Shannon's (1948) measure of information to quantify the rate of information flow in neurons. Shannon first developed the basic framework for his information measure in a classified memorandum for Bell Laboratories (see Shannon 1949). His primary concern in "A Mathematical Theory of Information" was to optimize information flow through physical channels by minimizing distortion. He was not concerned about the subject matter that people wanted to discuss, or even whether they were transmitting meaningful messages. As he put it, "semantic aspects of communication are irrelevant to the engineering problem" (Shannon 1948, 379). In applying Shannon's quantitative theory to the study of neurons, MacKay

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[6] Also see Miller (1953) for an early survey of information in psychology.

and McCulloch were decidedly *not* concerned with the "meaning" of the neural message, or the way that the neuron is able to communicate to the brain *about* the goings on in the outside world. Rather, they were examining the neuron as a channel for the transmission of information, and asking whether the neuron optimizes the rate of information flow. In other words, they wanted to know whether the neuron achieves the rate of information flow that is theoretically maximal, from an engineering standpoint (MacKay and McCulloch 1952, 128).

In borrowing terms and concepts from the communications industry, then, Adrian could be construed as being part of a tradition. But there is no reason to think that the political and technological context that made such "borrowings" intelligible and even fruitful in one era would be the same as the contexts that rendered those analogies intelligible and fruitful in others. The best way to approach what Adrian (and colleagues such as Forbes) "meant" by "information" and cognate terms, and the significance that these terms had on his laboratory practices, is to consider them in light of the First World War and the impact of the war on brain research and nerve physiology more generally.

That story centers crucially on a specific technology that the war made generally accessible, the vacuum tube. The vacuum tube was deployed during the war for the purpose of amplifying, detecting, and intercepting *coded messages*. The political history of the vacuum tube thus provided the immediate context in which Adrian progressively came to conceive of the nerve fibers and understand their operation in the 1920s. For Adrian, the kind of "information" carried by the nerve was "information" in *something* *like the sense of coded messages* – but with some important qualifications. Like Helmholtz, and unlike later theorists such as MacKay, Adrian believed that the main function of the sensory neuron was to transmit messages about the environment to the brain. He was not concerned, as later brain scientists would be, with analyzing the neuron as an informational channel and asking whether it optimized information flow. He wanted to know specifically what the neuron was "telling" the brain. Unlike Helmholtz, however, Adrian was equally preoccupied with the precise method of *coding*. That is, he attributed to the nerve a language-like structure that enabled it to perform a communicative role. This did not mean that he thought the nerve activity possessed an elaborate lexicon and grammar. Nor did it mean that he thought there was something in the brain corresponding to a "reader" or "interpreter." It meant rather that the nerve was able to tell the brain about what was "going on" in the world and it did so *by means of* modulating the specific pattern of action potentials it transmitted. This created a space for new kinds of questions to be asked of the neuron, such as questions regarding the abstract relationship between impulse and stimulus by virtue of which the former carried "information" about the latter.

3. The Vacuum Tube and the Political Context of Adrian's Work.

Adrian duly recorded his debt to the wireless communications industry in his 1928 book, *The Basis of Sensation*:

> Fortunately the detection of very small and very rapid electric changes has recently become a problem not confined to physiology, and our difficulties can be solved by the use of methods devised for wireless communication. When the academic scientist is forced to justify his existence to the man in the street he is inclined to do so by pointing out the essential part played by academic research in the development of our modern comforts. It is only fair, therefore, to point out that in this case the boot is on the other leg and the academic research had depended on the very modern comfort of broadcasting (Adrian 1928, 39).

By 1932, in his *The Mechanism of Nervous Action*, a book based on a series of lectures given to a general academic audience at the University of Pennsylvania, Adrian's emphasis on the centrality of communications technology to nerve physiology was even more pronounced:

> The advent of triode valve, or vacuum tube amplification has so altered the whole position that we can compare ourselves to a microscope worker who has been given a new objective with a resolving power a thousand times greater than anything he has had before. We only have to focus our instrument on the field to find something new and interesting (Adrian 1932, 5).

The vacuum tube played a major role during the 1914-1918 conflict for the amplification and detection of coded messages. The technology, which made Adrian's achievement possible, provided a material bridge that tied Adrian's work on nerve to the communications industry. In fact, wireless communications companies such as Western Electric often indirectly sponsored the research by loaning vacuum tubes to the laboratories (Frank 1994, 222; also see Kevles and Geison 1995; Finger 2004 for overviews of the use of the vacuum tube in nerve physiology). The vacuum tube, in a sense, brought this "informational" conception of the neuron into Adrian's laboratory.

In 1904 and 1905, the English physicist J. A. Fleming of the University of London patented the two-electrode vacuum tube – also referred to as the 'diode', 'oscillating valve', or 'Fleming valve' – for the detection of radio currents. The basic principles of Fleming's design were fairly simple.[7] The simplest vacuum tubes consisted of evacuated glass tubes that contained two electrodes – the 'filament' and the 'plate' – between which there was an electric potential. As temperature of the filament increased, it released a stream of electrons towards the plate, thereby setting up a current.

In 1907, the American inventor Lee de Forest improved Fleming's design by interposing a third electrode, or 'grid', between the filament and plate. By independently controlling the grid, one modulated the current that ran from the filament to the plate. The three-electrode vacuum tube – also known as the 'triode' or 'audion' – functioned as a powerful amplifier of radio signals as well as a detector. Engineers soon began to use the triode not only in wireless radio communication but also as a repeater for long-distance telephone signals. De Forest's improvement also set up a prolonged patent dispute between himself and J. A. Fleming. The vacuum tube was produced on a massive scale

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[7] See Fleming 1919; 1920; Van der Bijl 1920, and Chaffee 1933, for early histories and overviews of the technology; also Cardwell 1995, 381-384.

during the war. Many countries used it for the purpose of military communication, and it was in this context particularly that Alexander Forbes began developing his expertise.

Shortly after the war, several people seem to have independently arrived at the idea of using the vacuum tube for the detection of minute electrical disturbance in nerve. Perhaps in retrospect this should not seem surprising. As Adrian observed in 1928, the vacuum tube "was developed on a large scale in [World War I] and is now an article as widely advertised as the motor car or the safety razor" (Adrian 1928, 39). The German physiologist Rudolf Höber was the first to publish the results of using the vacuum tube for the amplification of nerve activity in 1919 (Höber 1919). In his "Ein Verfahren zur Demonstration der Aktionsströme [A Method for the Demonstration of the Action Current]", Höber described a way of supplementing the telephone with the vacuum tube (*Vakuumröhre*) for amplifying nerve impulses. The article primarily consisted of a description of sounds produced at different levels of amplification.[8] Höber claimed to have independently arrived at the idea of using the vacuum tube for this purpose: "*Dies hat mich auf den Gedanken gebracht, die Röhre beim Abhören der oszillatorisch verlaufen Aktionsströme mit dem Telephon zu verwenden* [This brought the idea to me to use the tube with the telephone for hearing the oscillating course of the action current]" (Höber 1919, 305). He was able to conduct his research by using amplifiers made briefly available to him by "*der Gesellschaft für drahtlose Telegraphie* [the corporation for wireless telegraphy]" (Höber 1919, 306).

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[8] Because these differences were not quantified, it is not clear what level of amplification Höber achieved.

In 1920, Alexander Forbes and his research assistant Catherine Thacher published the results of using the three-electrode vacuum tube in conjunction with the string galvanometer for the amplification of nerve activity. Horatio Williams, a physiologist at Columbia University, suggested the idea to Forbes in the spring of 1916 (Forbes and Thacher 1920, 409).[9] Forbes and Thacher were able to achieve a 45-fold amplification of nerve activity with the vacuum tubes or 'electron tubes' that the Western Electric Company lent them. Although Höber beat Forbes to publication, Forbes' 1920 paper with Thacher was pioneering in the way that it outlined a detailed protocol for its use.

The work of American nerve physiologists Herbert Gasser and H. S. Newcomer at Washington University in St. Louis shortly followed Forbes and Thacher's work. In 1921, Gasser and Newcomer described the results of both Höber's and Forbes and Thacher's work, but credited the idea of using the vacuum tube to supplement the string galvanometer to an A.S. Langsdorf, who suggested it to them in the spring of 1919 (Gasser and Newcomer 1921, 1). They achieved a significantly higher level of resolution of nerve activity (7000- to 8000-fold) by devising a three-stage amplification system. Another article by Gasser followed in 1922, in which he and Joseph Erlanger modified the arrangement through the innovative conjunction of the vacuum tube with the cathode ray oscilloscope rather than the string galvanometer, using tubes on loan from Western Electric (Gasser and Erlanger 1922). It was Forbes, however, who proved crucial for Adrian.

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[9] This claim is corroborated in Frank 1994, 221.

Forbes was from a well-to-do Boston family.[10] He was the grandson of Ralph Waldo Emerson and the son of president of Bell Telephone. After graduating from Harvard in 1910, Walter Cannon (then Chair of the Physiology Department) offered Forbes a permanent instructorship. Forbes went on to become a pioneer in the construction and application of physical techniques to the study of the nervous system. Shortly after graduating from Harvard Medical School, he spent a year at the University of Liverpool with the neurophysiologist Charles Sherrington. He occasionally visited Keith Lucas at Trinity College, where he also met Adrian. In Britain he became adept at electrophysiological instruments and, upon returning to Harvard, installed one of the first string galvanometers in the United States. His first two major publications came in 1915, in which he and Harvard medical student Alan Gregg (later Director of the Medical Sciences Division of the Rockefeller Foundation) measured the reflex arc in cats. Along with Lucas, Forbes was one of the first nerve physiologists who became primarily remembered for his technological accomplishments rather than his laboratory discoveries or theoretical innovations (which were not insubstantial).

In the summer of 1916, Forbes suspended his research at Harvard to volunteer for the U.S. Navy as a radio engineer. Not only did his private wealth make teaching unnecessary, but he was also particularly passionate about the war effort. As he confided to Adrian in an earlier letter dated July 1, 1915, “I feel a bit guilty about sitting still and letting you fellows fight our fight for us…I long to see [Germany] beaten so overwhelmingly that it will be an object lesson to prevent any nation ever planning such a

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[10] For biographical information on Forbes, see Davis (1965), Fenn (1969), Frank and Goetzl (1978), Frank (1994), Finger (2004), and Marcum (2006).

scheme again."[11] He converted his home into an amateur radio laboratory to familiarize himself with radio communication. He also took part in the Civilians' Naval Training Course, where he came into contact with the work of installing radio sets in Naval ships. He was enrolled as a lieutenant in the Naval Reserve in March of 1917, and was involved in harbor patrol (Forbes 1922). As a lieutenant, he worked on installing radio detectors into ships. His hope was that they would be used in the front lines of battle, to detect German submarines and hunt them down. Instead, they were used on a somewhat more humdrum, but important, task: as a homing device to guide ships under poor weather conditions.

Forbes never relinquished his fantasies of using the radio sets to help sink submarines. Instead, he fulfilled them by turning to fiction. He wrote a science-fiction novel, *The Radio Gunner*, which was published anonymously by Houghton Mifflin in 1924. *The Radio Gunner* was about a fictional world war set in the late 1930s. A power-hungry empire based in Constantinople gains the allegiance of Russia and vies for world domination. An aging American physicist, Jim Evans, installs radio devices in American ships. These devices have the purpose of detecting submarines, and transmitting and intercepting coded messages. Naturally, Evans helps to bring about the enemy's surrender through his technical savvy as well as through his friendship with Sam Mortimer, the Secretary of the Navy. Moreover, he does so in spite of a cast of villains, which include a fat, red-faced admiral who balks at the use of the new-fangled vacuum tubes of British manufacture. In some ways the book was prescient, because it articulated

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[11] Draft of a letter from Forbes to Adrian dated July 1, 1915 (Alexander Forbes Papers Box 1, Folder 2).

Forbes' growing conviction that future wars would be won or lost through communication strategy. As Evans tells his friend and confident Mortimer:

> The average naval officer takes far more interest in ordinance and gunnery than he does in communication…[but] just as the skill and wisdom of the gunnery officer direct the titanic force of the guns to the point where it is most telling, so the controlling mind, acting through communications, directs the first of the entire fleet; that's the field where the minimum energy will yield the largest return; put your best efforts in there (Forbes, 1924, 30-31).

In another passage, the protagonist celebrates the untold power of the vacuum tube:

> One improvement in particular, a new type of vacuum-tube transmitter which they had recently perfected, far surpassed anything that had yet been seen, and by its efficiency in eliminating interference it opened such extraordinary possibilities in the scope of fleet communications that without it the navy would be lagging sadly behind the more progressive Allies (Forbes, 1924, p. 58).

Forbes soon came to think that the vacuum tube should be the central player in nerve physiology as well as military strategy. When he resumed full-time work at Harvard in 1919, he immediately acquired vacuum tubes from Western Electric and applied them to the detection and amplification of the nervous message (just as he had hoped to do with coded messages in the war). Forbes did not hesitate to articulate the analogy between naval communication and the nervous system; moreover, he recognized that the analogy reached in both directions. Just as the Navy could be described as a kind of nervous system, so too could the nervous system could be described as little more than a set of relays that have the function of channeling messages. To Forbes, the nervous system itself *was* an elegant, efficient marvel of communications technology, the function of which was to transmit messages, signals, and, more generally, information about the environment from the peripheral nervous system to the brain. In a 1922 review piece on nerve physiology, he adroitly summarized the function of neurons: “The nerve fiber apparently exists for the purpose of transmitting messages to remote parts, rapidly, economically, and without modification” (Forbes, 1922a, p. 361).

Forbes played an instrumental role in getting the vacuum tube into Adrian’s hands. Not only did he give Adrian the idea for using the vacuum tube (See Hodgkin 1979, 24). He also spent five months with Adrian in Cambridge, from May to October of 1921, and arranged for the tubes to be shipped to Adrian’s laboratory. Forbes and Adrian were particularly interested in resolving the structure of sensory (rather than motor) impulses and applied the tube for detecting the afferent response in a cat’s femoral nerve (Adrian and Forbes 1922). They were unable to record from a single neuron, in part because they used only a one-stage amplification system and in part because of the problem of mechanically isolating a single neuron.

The following year, Adrian developed a friendship with the American physiologist Herbert Gasser. Their friendship was intimate enough that Gasser accompanied Adrian and his family on a skiing trip in Switzerland (Frank 1994, 229). By 1925, Adrian contacted Gasser to request detailed instructions regarding his powerful, three-stage amplifier. As noted above, in 1921, Gasser and his assistant Harry Newcomer described the results of their amplifier, which consisted of a sequence of vacuum tubes in which the output of the first was fed into the second, and so on. Instead of the 25- to 50-fold amplification eked out by Forbes, they achieved a robust 7000-fold amplification of the activity of the dog's phrenic nerve. Adrian had the three-stage amplifier built at Cambridge in January of 1925.

Adrian's apparatus, however, was importantly different from either Gasser's or Forbes'. Adrian conjoined the three-stage amplifier with the capillary electrometer instead of the string galvanometer or the cathode ray oscilloscope (see Adrian and Cooper 1925). Although the capillary electrometer was designed in the 1870s, Adrian's mentor Lucas had substantially improved it on the basis of principles derived independently by physicist George J. Burch of Oxford in 1890 and physiologist Willem Einthoven of Leiden University in 1894 (Frank 1988).[12] Thus, Adrian's use of the capillary electrometer became a lasting tribute to Lucas' influence.

Adrian's innovative instrumental arrangements quickly led to the Nobel-prize winning work with Zotterman – the recording of the electrical activity of a single sensory neuron. Shortly after this achievement, Adrian took every opportunity he could to extol the virtues of the vacuum tube. Intriguingly, the story of Adrian's first encounter with the

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[12] Its design and construction is described in Lucas 1909 and 1912; Lucas 1912 cites Burch 1890 and Einthoven 1894 for the basic principles.

tube became the stuff of legend in the Cambridge lab (Bradley and Tansey 1996, 222). By the 1930s, Adrian began circulating the story that Keith Lucas had given him the idea of using the vacuum tube, shortly before his untimely death. In the preface to his 1932 book, *The Mechanism of Nervous Action*, Adrian wrote:

> A few weeks before his death, [Lucas] talked to me of the great possibilities which might lie in the use of the thermionic valve for amplifying nerve action currents. His forecast was justified in a few years by the work of Forbes and Gasser: and these lectures deal with the use of the method at Cambridge for the study of the units of the nervous system. Had Keith Lucas lived, it is certain that the present stage would have been passed long ago; it is even possible that the method would have already served its turn (Adrian 1932, vii).

In 1914, Lucas set aside the manuscript he had been working on, which was revised and later published by Adrian in 1917 under the title *Conduction of the Nervous Impulse* (Lucas 1917) and left Cambridge to volunteer his services for the war as an aircraft engineer. He died in a plane accident in October of 1916 (Hodgkin 1979, 16).[13]

Shortly after recording the activity of the single neuron, Adrian began describing the sensory impulse as carrying “information,” as well as cognate terms such as “message,” “signal,” and even “code.” It is true that “information,” “message,” “signal,” and “code” are different terms with different senses. Yet Adrian did not seem to make fine

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[13] See Geison 1973 for a compact overview of Lucas’ life and work.

discriminations. For example, in some places the impulses are described as a code: “they transmit their messages to the central nervous system in a very simple way…the sensory messages are scarcely more complex than a succession of dots in the Morse Code” (Adrian 1932, 12). In others they are described as messages: “[T]he frequency of the discharge controls the intensity of the effect which the message produces” (Adrian and Bronk 1929, 145; also see Adrian 1931, 147; Adrian and Gelfan 1933, 275). Sometimes he uses “information,” “message,” and “signal” interchangeably: “[T]he Pacinian corpuscles…serve to convey information…signal the changes of pressure…take some part in the message” (Adrian and Umrath 1929, 145-147). For Adrian, the crucial factor was that the nerve impulse functioned *somewhat like a coded message*. It had a “semantic” function – to carry information about the stimulus – and it carried out this function by using a language-like structure, in the sense that it appropriately modulated it activity to convey this information.

Adrian’s reliance on this “informational” conception of the nerve is evident not only through his linguistic choices, but through the whole tenor of his research in the late 1920s. Very little of this work makes sense without this “informational” framework. In these years, Adrian’s goal was to demonstrate the near-universality of the basic principles of the nerve activity across different types of nerves and in different biological species. There were at least three such principles that he pursued. The first was the all-or none principle, according to which the amplitude of an impulse is independent of the strength of the stimulus which evokes it. The second was the principle of adaptation, whereby the firing rate of the nerve tended to decrease with the continued application of a constant stimulus (e.g., Adrian 1928, 29). The third was the principle that the frequency of a sequence of action potentials appeared to be some kind of exponential function of the intensity of the stimulus (e.g., Adrian and Matthews 1927, 392).[14] The crucial point is that Adrian interpreted each of these principles in *informational* rather than *mechanistic* terms.

4. Information at Work in Adrian's Lab.

Historians of science have amply documented the way that technological innovation drove early-twentieth-century neurophysiology. This shift toward technology went hand-in-hand with a seeming disciplinary reorganization of the field, as physiologists turned toward physicists, mathematicians, and electrical engineers, not only to help them design and construct their equipment but to articulate their research agendas and to generate and interpret data. Yet there was a tension, and even a contradiction, at the heart of nerve physiology, for along with the *physicalization* of the methods of nerve physiology there was an *etherealization* of the subject matter. The nerve impulse was dissolved into a flow of information; or, more accurately, questions about the physical mechanism of the nerve impulses were asked in tandem with questions about their information-bearing function.

Firstly, it is unnecessary to belabor the way in which the turn to technology was carried forth in terms of the fine-grained details of instrumentation. Robert Frank has already

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[14] Contemporary neuroscientists refer to this as 'rate coding' because the firing rate of the neuron is correlated with the intensity of the stimulus and thus, as it were, 'encodes' this feature (e.g., deCharms and Zador 2000).

provided the authoritative survey in this area. Questions about the nature of nerve activity were being supplanted by questions about the construction, improvement, and interweaving of diverse technologies for the production of images. As Frank puts it, "logic yielded to images created by instruments" (Frank 1994, 233). In some sense, Adrian's goal was to create a certain image, an image that would fundamentally alter the epistemic fortunes of the all-or none principle. The mere fact that we can easily articulate the aim of Adrian's laboratory practices as the production of a stable visual image – an image that could be reproduced in journals and newspapers, and disseminated to the world at large – amply demonstrates that the technology available to him dictated the kinds of questions that he asked and the format in which he could provide an acceptable answer.

Historian of science Paul Forman provides a more general way of sketching the changes that took place (Forman 2010). Forman has aptly described postmodernity (*qua* historical era) as consisting, in part, of an altered relationship between science and technology. A mark of modernity, in Forman's view, is the idea of technology as a *means* (that is, a mere method for tackling well-posed research questions). In postmodernity, however, technology assumed a kind of primacy; it became unmoored from any specific research question and became a resource for promoting *ad hoc* purposes.

Forman was mainly concerned with characterizing a specific historical shift in the relation between science and technology that marked the 1960s to the 1980s. But in some limited respects, his remarks characterize the changes in nerve physiology during the first half of the twentieth century. It was, perhaps, the first time that researchers became largely recognized for their technical accomplishments rather than their empirical discoveries. Two such individuals were Lucas and Forbes. Of course, the major accomplishments of this period of nerve physiology were not mere byproducts of improved instruments. As Frank (1994, 235) insists, Adrian's achievement can only be accounted for in terms of what he calls a “system,” which consisted in a unique confluence of laboratory instruments, ingenious experimental design, and biological materials.

The second aspect of this general transition was a disciplinary reorganization of physiology toward a greater reliance on the methods of the physicist, mathematician, and engineer. It is notable, in this regard, that each of the major players in the amplification of the nerve impulse worked closely with one (or more) engineers or physicists. Forbes collaborated with Horatio Williams; Adrian collaborated with Detlev Bronk; Joseph Erlanger collaborated with William Newcomer. In his correspondence with Forbes, Adrian humorously voiced his disappointment that he did not have the physical and mathematical acumen that his new research agenda demanded: “The electric response of nerve is really beginning to show something about itself now – it almost makes me wish I hadn’t gone off on to nerve endings and such like – but it will soon get into the realms of physics and chemistry and mathematics and I know my failings, or at least a few of them!”[15]

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[15] Letter from Adrian to Forbes dated April 29, 1929 (Alexander Forbes papers, Box 1, Folder 21).

This disciplinary reorganization was not limited to altered laboratory arrangements, but institutional and pedagogical changes as well. Forbes, in particular, was outspoken in his view that the technological changes in physiology should be matched by an institutional and pedagogical shift that would promote a greater reconciliation, if not total assimilation, of physiology into physics. In a 1920 opinion piece published in the journal *Science*, he lamented the disconnection between physiology and physics and even outlined a new field, "biophysics" (Forbes 1920). In an address to the Third International EEG Congress in 1953, Forbes heartily endorsed Sherrington's 1912 statement that the most important discoveries in nerve physiology would result from the biologists' use of the methods of the physicists.[16]

The turn toward viewing nerve activity as having the function of transmitting information was in some ways a product of this transition. That is because this informational conception of the neuron was made possible by technologies that were deployed for solving physical problems of measurement. Yet, in other ways, it represented an important countermovement, a trend in the opposite direction of physics. Somewhat ironically, the incorporation of the methods of the physicists contributed to a kind of *etherealization* of nerve activity. This is seen in the translation of the basic principles of the nerve activity into informational and teleological terms. When the electrical impulse was converted into information, researchers could start asking questions about the abstract nature of the "coding" relationship between impulse and stimulus. Ultimately, the study of this relationship could be absorbed into pure mathematics, as researchers

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[16] Forbes in *Third International EEG Congress 1953-Symposia* (Alexander Forbes papers, Box 48, Folder 1603).

could pursue the analysis of this neural code independently of its specific material basis (e.g., Rieke et al. 1997).

For Adrian, what was important was not only the physical nature of the impulse and the manner in which it is transmitted through the nerve, but the abstract relationship between the pattern of the impulse and the pattern of the stimulus by virtue of which the former can be said to transmit information about the latter. For example, one indelible hallmark of this shift of interest toward “informational” features of the neuron was the almost seamless manner in which Adrian, and to some extent Forbes, could translate the basic physical principles of the neuron into an informational and even teleological context. This “translation” can be seen with each of the three foundational principles of nerve activity: the all-or-none principle, adaptation, and the principle that eventually came to be known as “rate-coding.”

Prior to the 1920s, the all-or-none principle – that the amplitude of the impulse is independent of the strength of the stimulus that set it up – merely described a brute physical fact about the structure of the nerve impulse and the manner in which it was perpetuated across the fiber. In Adrian's hands, however, the principle became a constraint on the syntax by which the message must be formulated. What was important was that the nerve impulse had a discrete, rather than continuous, format. This gave it its language-like structure. In his 1928 *The Basis of Sensation*, Adrian explained:

> The message which it transmits must consist of a series of impulses which cannot

> recur at more than a certain frequency. To take an analogy: the nervous message may be likened to a stream of bullets from a machine gun, it cannot be likened to a continuous stream of water from a hose (Adrian 1928, 27).

A few years later, Adrian elaborated this linguistic analogy and tied it to the metaphor of coding:

> If these records give a true measure of the activity in the sensory nerve fibers it is clear that they transmit their messages to the central nervous system in a very simple way. The message consists merely of a series of brief impulses or waves of activity following one another more or less closely. In any one fibre the waves are all of the same form and the message can only be varied by changes in the frequency and duration of the discharge. In fact the sensory messages are scarcely more complex than a succession of dots in the Morse Code (Adrian 1932, 12).

The principle of adaptation – that given an unchanging stimulus, the neuron would eventually stop producing impulses – underwent a similar shift, and even assumed a strong teleological orientation:

> So, if we keep still, we cease to be disturbed by sensations from our limbs because they have ceased to send us any messages...[But if the] environment is continually changing, the receptors continue to send us messages, and we cannot withdraw our attention from them though we should be very glad to do so...

> (Adrian 1928, 99).

When nothing was changing there was no point continuing to inform the brain about it. Thus, the nerve stopped sending signals. Adaptation was seemingly an economical defense against the pointless, and metabolically costly, production of redundant messages.

The third, and most important principle of nerve transmission, is one that is almost impossible to even formulate without using the language of information. What Adrian recognized about the structure of the nerve impulse was that, in some sensory neurons, the frequency of the nerve impulse approximated an exponential function of the intensity of the external stimulus (Adrian and Matthews 1927, 392). For Adrian, this was not a mere mathematical function that demanded a mechanical explanation. This was the primary method, or vehicle, by which the nerve communicates to the brain about the changes in the stimulus: "In both [the motor and sensory nerve] the frequency of the discharge controls the intensity of the effect which the message produces and is itself controlled by the intensity of excitation" (Adrian and Bronk 1929, 145). As a result of these considerations, Adrian's use of the language of "information" should not be seen as an incidental metaphor, but part of his basic "system" for making sense of the activity and function of the nerve.

5. Conclusion.

The foregoing has attempted to do three things by focusing on Adrian in his role in the nerve physiology of the 1920s. First, it has begun to fill an important gap in the history of the interaction between nerve physiology and the communications industry, particularly with respect to these “borrowings” of concepts and procedures from communications into physiology during the interwar period. Adrian, and to some extent Forbes, did much to elaborate this basic “informational” interpretation of the nerve impulse. Additionally, it has attempted to identify the specificity of Adrian's use of “information,” and its cognates, with respect to the idea of a coded message. There are two aspects of Adrian’s usage: first, that the nerve impulse transmits information *about* the external stimulus to the brain, and second, that it does so by modulating its inner structure in a predictable way. This gives the nerve structure a language-like character, though Adrian never attempted to perfect the analogy by postulating a fixed lexicon, grammar, reader, or interpreter.

Secondly, it has elucidated one aspect of the political and technological context for this “informational” transition, namely, Adrian’s use of the vacuum tube. The vacuum tube was mass-produced during the war for the purpose of military communication, and primarily for the amplification and interception of coded messages. Forbes himself, fascinatingly, decided to turn to fiction to articulate the systematic analogies between naval communication and the nervous system. The vacuum tube carried with it the memory of these practices like a stubborn residue.

Finally, it has attempted to make sense of this informational shift in terms of the broader transitions that took place in the relationship between science and technology itself. There were three very general features of this transition. The first was a shift toward technological innovation, and in the way that technological innovation shaped the kinds of questions that could be asked in the kinds of answers that could be given. Secondly, this transition toward technology brought with it a disciplinary and even institutional reformation of physiology in the direction of embracing physics, mathematics, and electrical engineering. Thirdly, and ironically, this physicalization of *method* ran up against an etherealization of *subject matter*, as the basic structure and function of the nerve impulse was translated into an informational and even teleological framework.

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