The Introduction of Information into Neurobiology

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The first use of the term ‘‘information’’ to describe the content of nervous impulse occurs in Edgar Adrian’s *The Basis of Sensation* (1928). What concept of information does Adrian appeal to, and how can it be situated in relation to contemporary philosophical accounts of the notion of information in biology? The answer requires an explication of Adrian’s use and an evaluation of its situation in relation to contemporary accounts of semantic information. I suggest that Adrian’s concept of information can be to derive a concept of arbitrariness or semioticity in representation. This in turn provides one way of resolving some of the challenges that confront recent attempts in the philosophy of biology to restrict the notion of information to those causal connections that can in some sense be referred to as arbitrary or semiotic.

1. Introduction. The beginning of the information era in neurobiology—that is, when information became an explicit theoretical and quantitative concept—is usually traced to the period immediately following the publication of Shannon’s (1948) landmark paper. The concept of information described there spread rapidly throughout psychology in the early 1950s (Miller 1953), and began to come into theoretical use in the neurosciences in the 1950s (MacKay and McCulloch 1952). However, the first use of the term ‘‘information’’ to describe the content of nervous impulse occurs twenty years prior to Shannon’s work, in Edgar Adrian’s *The Basis of Sensation* (1928). *The Basis of Sensation* is based on a series of lectures for a general scientific audience that describe the research leading up to his major scientific achievement, which was the recording of the electrical activity of a single sensory neuron:

> Gotch and Keith Lucas, by their analysis of the ‘‘refractory period’’ in nerves, gave us for the first time a clear idea of what may be called the functional value of the nervous impulse. They showed what the nerve

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> fibre can do as a means of communication and what it cannot. . . . It is of the first importance in the problems of sensation, for it shows what sort of information a sense organ can transmit to the brain and in what form the message must be sent. (Adrian 1928)

"Information" recurs occasionally throughout the text, and is generally associated, as it is above, with the transmission of messages. Although, at least throughout the 1920s and early 1930s, the term "information" does not appear in Adrian's specialized neurobiological writings to describe the content of nervous impulse, the notion that the structure of nervous impulse constitutes a type of message subject to certain constraints plays an important role in many of his writings throughout the period.

The appearance of the concept of information in Adrian's work raises at least two important questions. The first is interpretive: given that Adrian does not offer an explicit definition or analysis of the concept of information, what concept of information does he appeal to? The answer to this question requires an explication of his concept of information insofar as it can be reconstructed from the relevant texts (Sections 2 and 3). The second problem is evaluative and follows upon the first: given this explication, how can Adrian's concept of information be situated in relation to more contemporary philosophical accounts of a semantic notion of biological information (Section 4)?

According to the explication that will be provided below, Adrian's concept of information can be defined by the following three conditions:

A given system *S* (for example, a sequence of action potentials) is an information carrier $=_{\mathrm{df}}$ *S* has:

(C_1) *Quasi-discreteness:* *S* can be arranged into a sequence of discrete units that are separated by finite gaps or intervals. This condition constitutes a *syntactical constraint,* because it specifies the acceptable form of syntax that an information carrier must have.

(C_2) *Differential value:* Differences in *S* are strongly correlated with differences in some feature of the stimulus that produces it. This condition constitutes a *semantic constraint,* because for Adrian, this differential value is responsible for the capacity of a sequence of action potentials to *represent* the stimulus.

(C_3) *Medium independence:* The structure of *S*—for example, the temporal relations that obtain between the units of a sequence of action potentials—can be instantiated across a wide range of physical mechanisms.

As will be shown in Section 4, condition (C_2) of Adrian's concept of information, along with the premise that the differential value of the sequence is the basis of its semantic or representational value, can be used to derive a concept of arbitrariness. This will be referred to as a *semiotic constraint,* because arbitrariness tells us what it is for a given signal to be a *sign for* a given source. This derivation, based on semiotic principles drawn from structural linguistics and clarified by neurobiological examples, provides one way of resolving some of the challenges that confront recent attempts in the philosophy of biology to restrict the notion of information to those causal connections that can, in some sense, be referred to as arbitrary or semiotic.

2. The Birth of Single-Neuron Electrophysiology. This section will describe how Adrian solved the problem of measuring the electrical activity of a single sensory neuron, and how he consequently pursued the newly opened field of research to accumulate evidence for the universality of the structure of the nervous impulse. This structure, in turn, provided the material for analogies between the transmission of messages in artificial systems of communication and the transmission of impulses in the nervous system, thereby providing a rationale for the extension of the concept of information from artificial systems of communication to include some biological systems.

Adrian is credited today as having revealed the broad generality of some of the basic structures of nervous transmission (Rieke et al. 1997; Strong et al. 1998; Buracas and Albright 1999). The first is the "all-or-none" principle, according to which the amplitude of the action potential is independent of the intensity of the stimulus that evokes it. Above a certain threshold of intensity, a sequence of action potentials of constant amplitude will be initiated, while below that threshold the stimulus will not elicit an action potential. The second is the principle of "rate-coding," according to which the frequency of a sequence of action potentials is an exponential function of the intensity of the stimulus that elicits it. The third is the principle of "adaptation," according to which the frequency of the sequence decreases, and eventually halts altogether or returns to some background rate, with the continued application of a stimulus of constant intensity. Although some restrictions on the generality of the all-or-none principle have been found (many interneurons operate exclusively through graded potentials, for example), and rate coding alone is not sufficient to carry all of the representational content transmitted by a neuron (deCharms and Zador 2000), the three principles have not been significantly revised.

Although the all-or-none principle was known to hold of some motor neurons by the time of Adrian's work in the early 1920s, there was no practical way of assessing whether the all-or-none principle generally obtains in sensory neurons without reducing the bundle of fibers to a number that is analytically tractable. By the mid-1920s, no method was known for isolating a single sensory neuron in order to record its activity.

This difficulty was surmounted in 1925 by Adrian during his collaboration with Yngve Zotterman by using a nerve attached to the sternocutaneous muscle of the frog, *Rana temporaria,* that contains fifteen to twenty-five individual fibers. The strategy, which Adrian attributes to Zotterman, was to gradually cut away small strips from the muscle, until at the end of this process, they would be left with a strip of muscle connected only to a single neuron within the bundle. This process led to a gradual simplification of the initially erratic wave recording (produced by the capillary electrometer and initially representing the electrical activity of several sensory neurons) to one of constant frequency and amplitude. On the basis of the improbability of precise synchrony arising from the action of more than one sensory neuron, Adrian claimed to have represented a sequence of impulses produced by a single sensory receptor (Adrian and Zotterman 1926).

The ability to measure the impulse of a single sensory neuron opened a new field in neurobiology that Adrian vigorously pursued. The results of the research undertaken by Adrian and various collaborators between early 1926 and early 1929 are represented in three major series of articles all of which appear in the London *Journal of Physiology.* Throughout this period, Adrian was able to show that the three basic principles of nervous transmission—the all-or-none principle, rate-coding, and adaptation—obtain among several types of sensory receptors, across several biological taxa (Adrian 1926, Adrian and Matthews 1927), as well as among motor neurons (Adrian and Bronk 1929). The ubiquity of the structure of the nervous impulse implies the *medium independence* (C_3) of the sequence: that the temporal structure of the sequence can be instantiated across a wide range of physical mechanisms. (Maynard Smith 2000 makes a similar appeal to the principle of medium independence to justify the biological extension of the concept of information.)

3. Explication of Adrian's Concept of Information. The content of Adrian's concept of information, as indicated in Section 1, can be specified by three independently necessary and jointly sufficient conditions: (C_1) quasi-discreteness (syntactic constraint), (C_2) differential value (semantic constraint), and (C_3) medium independence. The following will show how these first two conditions emerge from the research described in the previous section, and are implicit in Adrian's writings from the period. The emergence of condition (C_3) has been described in the previous section as a consequence of the progressive universalization of the structural features of nervous impulses.

In his *The Mechanism of Nervous Action* (1932), a book written on the basis of a series of lectures given at the University of Pennsylvania, Adrian implicitly appeals to a principle of quasi-discreteness (C_1) by drawing an analogy between the structure of nervous impulse and the syntax of the Morse code:

> If these records [of the sequence of action potentials] 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)

This passage suggests an important *syntactic* property that is shared by the transmission of messages in artificial systems of communication and the transmission of sequences of action potentials, which is the *quasi-discreteness* of the sequence: a set of physical impulses is amenable to analysis as a sequence of discrete units that are separated by finite intervals of variable length. Note, furthermore, that the property of quasi-discreteness follows from the all-or-none principle, insofar as a finite interval must occur between any two adjacent action potentials. This does not, however, imply that quasi-discreteness should play a role in a proper explication of a semantic concept of information. The prevalence of graded potentials in interneuronal signaling, for example, provides reason to reject the relevance of this condition.

The principle of quasi-discreteness, however, is typically characterized by Adrian as a *limitation* on the information-carrying capacity of the nervous system, and not itself as the feature that explains its representational or semantic content. That Adrian's concept of information does involve a *semantic* component is evident by his association of the notion of information with the notion of sending a message. Presumably the "functional value" of a nervous impulse, described in the first passage above, alludes to its capacity for *representing* features of the stimulus that elicits it.

The intuitive concept of representation can be given partial explication by the criterion of differential value (C_2)—that differences in the system (e.g., sequence) are strongly correlated with differences in some feature of the stimulus that produces it. This is because differential value captures two important intuitions about the concept of representation. The first is that if there are differences in the representational element, then there are differences in the state of affairs being represented. I will refer to this as the structural aspect of representation. The second is that the representational element stands in some appropriate causal relation to the state of affairs being represented. I will refer to this as the causal aspect of representation.

However, the concept of differential value must be analyzed in turn in order to show how it can be distinguished from a standard causal account of information, and this involves an elaboration of the sense of "differential" involved. This sense of "differential" should be consistent with the locution that, for example, the sequence of action potentials *specifically encodes differences* in the stimuli, rather than constant states. One plausible way of elaborating the notion that the sequence specifically encodes differences in the stimuli is through the claim that a nonchanging stimulus will stop producing a sequence of action potentials, and therefore that *only* changes in the environment will elicit a sequence of action potentials, much in the same way that a completely predictable system will not contain information in the communication-theoretic sense.

That a sequence of action potentials possesses differential value (C_2) follows from the conjunction of the principle of rate coding with the principle of adaptation. While the principle of rate coding entails that the frequency of the sequence of action potentials is an exponential function of the magnitude of the stimulus, the principle of adaptation entails that upon application of a constant stimulus, the frequency of the sequence of action potentials will diminish, and eventually such outputs will stop being produced. Hence the relation between the sequence and stimulus is differential: *differences* in the frequency of the sequence of action potentials map onto *differences* in the intensity of the stimulus that produce them, and not onto constant states of the stimulus.

That, for Adrian, the differential value of the sequence captures the sense in which the sequence can be said to *represent* some feature of the stimulus, and hence constitutes a semantic condition, becomes clear in the context of his remarks on the phenomenology of sensation:

> 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. . . . It is easy to multiply instances of sensations fading owing to the adaptation of the receptors to a constant environment. (Adrian 1928)

In this passage, Adrian draws on both principles of rate coding and adaptation in order to suggest a connection between the structure of the sequence and the nature of sensation—only changes in the environment are represented by the system, and hence presented to consciousness, rather than constant states. In the next section, the condition of differential value will be used to derive a concept of arbitrariness in representation. It is this element of arbitrariness that allows one to say that the relation between the two objects in the system is semiotic, that is, that the one is a *sign for* the other.

4. Biological Information and Arbitrariness. In 2000, *Philosophy of Science* published an article by John Maynard Smith entitled "The Concept of Information in Biology," along with commentaries written by Kim Sterelny, Peter Godfrey-Smith, and Sahotra Sarkar. One of the points of agreement that runs throughout the articles is that any concept of information that serves as an adequate explication of the sense in which, for example, genes contain information, should be restricted to those causal connections that can be referred to as "arbitrary" or "symbolic." The notion of arbitrariness sets up a *semiotic* constraint on the concept of information, insofar as it tells us what it is for a given signal to be a *sign for* a given source.

What justifies the claim that the relation between genes and the proteins they code for is arbitrary or symbolic is the idea that there is no chemical necessity concerning which nucleotide triplet codes for which amino acid residue. That CAC codes for histidine is a contingent biological fact; the mapping relation that obtains between the two series *could have been* reassigned. The inclusion of a semiotic restriction on the concept of information, however, does not resolve a problem so much as it opens one: how can arbitrary causal connections appear in nature? The problem is twofold. On the one hand, if nature is deterministic in its operations, at least on or above the macromolecular level of the biological hierarchy, this determinism appears to render such arbitrary causal relations impossible. A second problem is that even if the concept of an arbitrary causal connection could be elaborated so as to remain consistent with determinism, it would appear that the very *arbitrariness* of this relation is inconsistent with its *systematicity,* in the sense that the set of assignments between the two series is predictable and widespread.

There appears to be two directions in which the concept of an arbitrary causal connection—the idea of a causal connection that "could have been" different—can be explicated in manner that is consistent with determinism and systematicity. The first involves an appeal to historical considerations. Sarkar, in his commentary, explains the emergence of the arbitrariness of the genetic code by characterizing the code as a "frozen accident" (Sarkar 2000), thereby appealing to the historically *contingent* conditions from which the system emerged, where these conditions cannot be predicted on the sole basis of a *general* biological or ecological theory.

The second direction involves an appeal to structural features inherent in the mechanism that mediates the relation between the two orders, rather than the historical context from which the code emerged. In the case of a natural language, for example, the arbitrariness of the relation between a given signifier and a given signified can be understood as being due to the dependence of this relation upon a given convention. If this convention changes, the assignments between the two series would be altered, or a new set of signifiers would be introduced, etc. Hence the interposition of a mediating device that can change the mapping relation between the two series can be invoked to explain the absence of any inherent "affinity" between the units of the two series, and historical features would be strictly speaking unnecessary to explicate and justify the sense in which the relations are arbitrary.

Such a structural account is implicitly given by Sterelny in his commentary. In order to exclude cytoplasmic factors from being denominated as "information carriers," Sterelny introduces the notion of a "reader," that is, an intermediary between two systems that can reliably map differences in the one series onto differences on the other. An example of such a reader is the regulatory gene *eyeless,* which, when situated in a mouse, reads instructions from other (structural) genes and creates a mouse eye, and when transplanted into a fruitfly, produces a compound, fruitfly eye. It is by virtue of this capacity to "systematically map *differences* in structural genes onto *differences* in phenotypes" that such intermediaries allow for the possibility of unlimited or "code-based" rather than limited or "sample-based" systems of heredity (Sterelny 2000). What is important in this context is that the mechanism be sensitive to differences and change its output accordingly.

As will be seen, the arbitrariness condition and the differential value condition specified above bear a close conceptual relation to one another. For the originator of structural linguistics, Ferdinand de Saussure, these two conditions are inseparable and constitute the inherent structure of signification: "*Arbitrary* and *differential* are correlative qualities" (Saussure 1966). Saussure, in fact, attempts to show that each entails the other. If the relation between the signifier and signified is arbitrary—in other words, if there is no intrinsic connection between the two levels—then the semantic value of a given segment of language can only be based on its difference from other such segments, or as he puts it, its "noncoincidence with the rest" (1966). Conversely, Saussure derives the arbitrariness of language from its differential value:

> It is precisely because the terms *a* and *b* as such are radically incapable of reaching the level of consciousness—one is always conscious of only the *a*/*b* difference—that each term is free to change according to laws that are unrelated to its signifying function. (1966)

This arbitrariness is exemplified by the difference between two oppositions: "yes/no" and "ja/nein." If the representational value of the respective sets of symbols is based on the oppositional structure set up between them, then the use of a particular symbol to denote a particular quality (e.g., "yes" to denote affirmation) is arbitrary: the convention could be changed in such a way that the one pair is substituted for the other or the relation reversed. It is this converse implication that I would like to emphasize, since it allows a concept of structural arbitrariness to be drawn from Adrian's concept of information as explicated in the previous section.

Abstractly put, suppose that the representational value of a sequence of action potentials is solely based on its differential value—that differences in the system strongly correspond to differences in the intensity of the stimulus that produces it. Then, following Saussure's logic, there need not be a fixed set of assignments between a given firing rate r_i and a given stimulus intensity s_i in order for the representational value of the sequence of action potentials to remain intact. For example, suppose a stimulus of intensity s_i elicits a firing rate r_i from a neuron. Then s_i is held constant, and by the principle of adaptation, the firing rate is reduced (say, to r_{i-1}). Upon increasing the stimulus to s_{i+1}, the firing rate may return to r_i, its initial value. This case makes clear that there need not be a temporally invariant and one-to-one mapping from a given stimulus intensity to a given firing rate, and hence that the neuron can perform the role of a "reader" that is capable of changing the mapping relations between the two series. The assignments that obtain at a given time can be altered, and in this sense they are arbitrary. (Dretske 1986 provides an account of a similar type of representational complexity by appealing to a mechanism that transforms the mapping relation between stimuli and response over time. According to Dretske, such a mechanism would constitute a necessary but not sufficient condition for the claim that a given stimulus can be misrepresented.)

The distinction between arbitrary and nonarbitrary causal relations can be exemplified by two different mechanisms of auditory perception: the tympanic membrane and the hair cells of the inner ear. The rate at which the tympanic membrane vibrates in response to a stimulus is a mechanical consequence of the rate of oscillation in the air pressure that affects it: if the air pressure oscillates at n cycles per second, the tympanic membrane will vibrate at n times a second. The air pressure that mediates this process is not a "reader," because it is not specifically sensitive to *differences:* in the absence of a mechanism of adaptation, the steady vibration of the tympanic membrane in response to a fixed oscillation in air pressure can continue for an indefinite period of time.

The adaptability of the hair cells that line the epithelia of the inner ear organs provides a sharp contrast to the tympanic membrane. The bundle of stereocilia that arises from the apical end of the hair cell may facilitate adaptation in different ways. Deflection of the bundle of stereocilia is mechanically responsible for stretching ion pores in the stereocilia, allowing a cation current to pass into the cell. According to one model of adaptation, dubbed the "motor model" (Gillespie and Corey 1997), the tension induced by a constant level of deflection eventually causes an intracellular myosin block, which usually rests within the tip of the stereocilia, to shift downward. This shift causes the ion pore to partially close, thereby decreasing the firing rate of the neuron and changing its sensitivity to continuing stimuli.

According to a second model of adaptation (Crawford et al. 1991), intracellular calcium ions that enter the basolateral membrane of the hair cell when the cell is depolarized migrate toward the apical end of the cell. The increase in intracellular calcium concentration promotes the closed conformation of the ion pores in the stereocilia. These two models need not be inconsistent with one another (Eatock 2000), and both leave open the possibility of other sites of adaptation within the same cell. For example, one locus of adaptation may reside within the cell body, coming about by depletion of the glutamate-carrying synaptic vesicles (Furukawa and Matsuura 1978).

Due to these mechanisms of adaptation, the neuron continually recalibrates its sensitivity to different background levels of stimulus intensity. As a consequence, the neuron, whose maximum firing rate is relatively limited (to about 1000 action potentials per second), is able to represent an enormous range of variation in the stimulus. This system of representation would be impossible if there were a temporally invariant and one-to-one set of assignments between a set of stimuli and a set of firing rates.

The relation of arbitrariness that obtains between a given sequence of action potentials and a given stimulus intensity, then, can be accounted for by a structural concept of arbitrariness. By using Adrian's concept of information, then, the semiotic constraint need not be set up as an additional and independent criterion for being an information-carrier.

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