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Information Theory is Abused in Neuroscience

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In 1948, Claude Shannon introduced his version of a concept that was core to Norbert Wiener's cybernetics, namely, information theory. Shannon's formalisms include a physical framework, namely a general communication system having six unique elements. Under this framework, Shannon information theory offers two particularly useful statistics, channel capacity and information transmitted. Remarkably, hundreds of neuroscience laboratories subsequently reported such numbers. But how (and why) did neuroscientists adapt a communications-engineering framework? Surprisingly, the literature offers no clear answers. To therefore first answer "how", 115 authoritative peer-reviewed papers, proceedings, books and book chapters were scrutinized for neuroscientists' characterizations of the elements of Shannon's general communication system. Evidently, many neuroscientists attempted no identification of the system's elements. Others identified only a few of Shannon's system's elements. Indeed, the available neuroscience interpretations show a stunning incoherence, both within and across studies. The interpretational gamut implies hundreds, perhaps thousands, of different possible neuronal versions of Shannon's general communication system. The obvious lack of a definitive, credible interpretation makes neuroscience calculations of channel capacity and information transmitted meaningless. To now answer why Shannon's system was ever adapted for neuroscience, three common features of the neuroscience literature were examined: ignorance of the role of the observer, the presumption of "decoding" of neuronal voltage-spike trains, and the pursuit of ingrained analogies such as information, computation, and machine. Each of these factors facilitated a plethora of interpretations of Shannon's system elements. Finally, let us not ignore the impact of these "informational misadventures" on society at large. It is the same impact as scientific fraud.

Keywords: Shannon, information theory, neuroscience, communication, observer, decoding, metaphor, machine

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1. Introduction

In 1948 Norbert Wiener wrote the foundational book *Cybernetics* (1948/1961). He considered *information* to be crucial to cybernetics. That same year, Claude Elwood Shannon formalized information theory (Shannon, 1948). The following year,

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Shannon expounded upon it in a book that was co-authored and introduced by Warren Weaver (Shannon & Weaver, 1949). Shannon's information theory quantified two desired performance measures, *channel capacity* and *information transmitted.* The latter was eventually re-labelled as *mutual information* (e.g., Cover & Thomas, 1991). Information theory became the focus of tens of thousands of communications-engineering publications.

Information theory is a mathematical model. The frame of any mathematical model is its assumptions. In particular, Shannon's information theory was predicated upon a *general communication system* (Shannon, 1948; Shannon & Weaver, 1949), an assumed physical framework having six elements, namely: 1. "An *information source* which produces a message or sequence of messages to be communicated to the receiving terminal" (Shannon, 1948, p. 380), (2) "A *transmitter* which operates on the message in some way to produce a signal suitable for transmission over the channel" (p. 381), (3) a *channel*, where "The *channel* is merely the medium used to transmit the signal from transmitter to receiver" (p. 381), (4) a *receiver*, where "The *receiver* ordinarily performs the inverse operation of that done by the transmitter, reconstructing the message from the signal" (p. 381), and (5) a *destination*, such that "The *destination* is the person (or thing) for whom the message is intended" (p. 381). There was also (6) a *noise source*. Figure 1 illustrates the general communication system.

Shannon (1948) stipulated that messages sent through his general communication system are groups of symbols, such as letters arranged into words and then into sentences. The information transmitted in a message, I_t, can subsequently be calculated, because symbols have probabilities. Consider *n* possible *events* (symbols sent); the one that occurs is the outcome, which is uncertain if $n > 1$ unless the system is perfect. When each event has a known probability of occurrence, p_i, where $i = 1, \ldots, n$, such that $\sum_{i=1}^{n} p_i = 1$, then the overall signal uncertainty (signal information) I_S (using *S* for *symbol sent* or *signal*) is

$$I_S = -K \sum_{i=1}^{n} p_i \log p_i \; (K > 0)$$

The value of *K* is a matter of convention; Shannon set $K=1$. Denoting symbols by *k*,

$$I_S = -\sum_{k} p(k) \log p(k)$$

The algebra is kept simple by stipulating that any symbol received is from the set of symbols that can be sent. But the system is noisy; not all symbols will be received as sent. Information transmitted, I_t, can be calculated knowing (a) what symbols *k* (events) were sent, (b) what symbols *j* (outcomes) were received, and (c) the number of times a symbol sent as *k* was received as *j*, denoted N_{jk}. The latter numbers form an array called the *confusion matrix*. Figure 2 shows the confusion matrix for a total number *N* of symbols sent. Denoting the probability that *k* was sent to be

$p(k) = N_{.k}/N$, and denoting the probability that k was sent if j was received to be $p_j(k) = N_{jk}/N_{j.}$, we can now express the *signal equivocation/entropy*, E_S, as

$$E_S = -\sum_j \sum_k p_j(k) \ \log p_j(k)$$

and the information transmitted, I_t, as

$$I_t = I_S - E_S = -\sum_k p(k) \ \log p(k) \ + \ \sum_j \sum_k p_j(k) \ \log p_j(k)$$

Note well that these are averages, taken over the course of the entire *message*. The base of the logarithms is a positive integer. Traditionally, the base is set to 2. Information transmitted is thus in binary information units per symbol, *bits/symbol*. Note also that $I_S \geq I_t \geq E_S \geq 0$, and that "noiseless" transmission would mean $I_t = I_S$.

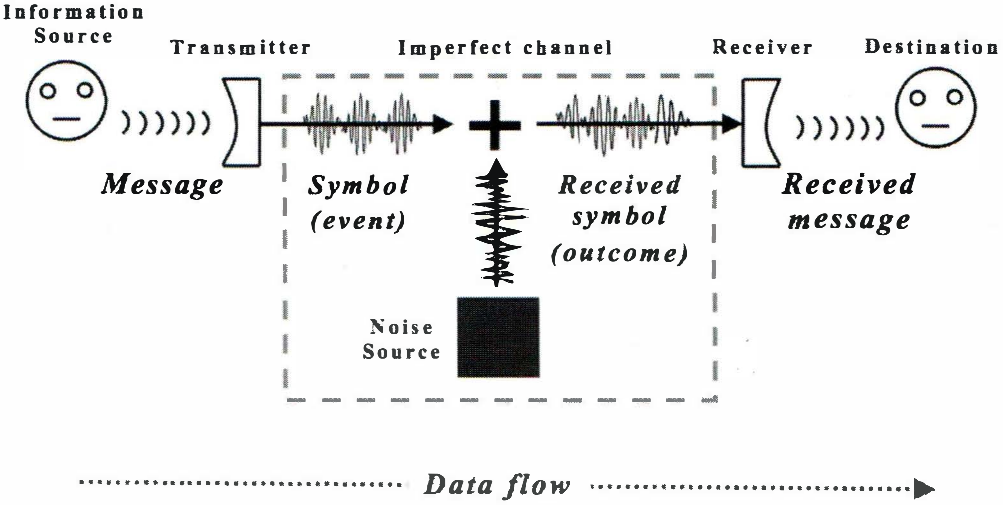

Figure 1. Shannon's general communication system. Data, in the form of messages relayed using symbols, flows from source to destination. The data itself may or may not have meaning to any persons involved.

Shannon's model, summarized above, was concerned with man-made systems. Why, then, apply Shannon's information theory to neurons? The rationale proceeds as follows. When a sensory stimulus is applied to an organism that has neurons connected to sensory receptors, firing of voltage spikes may be evoked in those neurons. That is, the number of voltage spikes evoked during the *spike-counting time*, some sub-interval of the stimulus's duration, will change systematically as some stimulus characteristic is changed. But so may the instantaneous spike-firing rate, or the latency of the first stimulus-evoked spike, or the intervals between spikes, or "the principal components of the temporal waveform of the response" (Nizami, 2014b, p. 2), and so forth. Nonetheless, the most commonly-used measure of the stimulus-evoked neuronal response is the mean stimulus-evoked count of voltage spikes, estimated over repeated identical presentations of the stimulus. The mean spike-count tends to smoothly, systematically change in response to smooth, systematic stimulus change(s). Of course, what determines subjective experience may be the pattern of neurons that are engaged, rather than the transmission along any particular neuron. Nonetheless, the literature has emphasized the activity of single neurons, presumably because this has been easier to do, but also because of a belief that the whole cannot be understood without understanding the parts.

There is some inherent variability (stochasticity) in any sensory neuron's response to changes in some stimulus characteristic(s); that is, the neuron's response to the sensory stimulus seems inherently confused. That confusion is what neuroscientists believe that they can quantify using information theory. To neuroscientists, the stimulus characteristic being varied (e.g., its intensity) is the Shannon *symbol sent* (event). Hopefully, the stimulus will evoke in the neuron, on average, a predictable *symbol received* (outcome). The difference between any event and the resulting outcome is attributed by neuroscientists to the probabilistic nature of spike firing, often interpreted as noise.

	Symbol sent (event)						
Symbol received (outcome)	**1**	**2**	**-**	**k**	**-**	**n**	**Row totals**
1	N_{11}	N_{12}	-	N_{1k}	-	N_{1n}	$N_{1.}$
2	N_{21}	N_{22}	-	N_{2k}	-	N_{2n}	$N_{2.}$
-	-	-	-	-	-	-	-
j	N_{j1}	N_{j2}	-	N_{jk}	-	N_{jn}	$N_{j.}$
-	-	-	-	-	-	-	-
n	N_{n1}	N_{n2}	-	N_{nk}	-	N_{nn}	$N_{n.}$
Column totals	$N_{.1}$	$N_{.2}$	-	$N_{.k}$	-	$N_{.n}$	**Sum** =N

Figure 2. Shannon's Information Theory Confusion Matrix.

Any present conclusions about the appropriateness of information theory in neuroscience do not intrinsically depend upon the particulars of the neuronal response measure, but rather on how it is employed in calculating information transmitted, I_t. The present conclusions also apply under a particular technique that is slowly being adopted in the laboratory, namely, calculation of I_t from a vector of responses, representing an ensemble of neighboring neurons. What matters is that neurons are involved, not their particular number.

The random processes underlying voltage-spike-generation are usually assumed to be unchanging with time (stationary), as presumably reflected in unchanging probability-density functions of either the voltage-spike counts or the time intervals between the spikes, or some other proxy.

2. Problem and Method

Joseph C. R. Licklider, a progenitor of the Internet, noted in 1951 that "It is probably dangerous to use this theory of information in fields for which it was not designed, but I think the danger will not keep people from using it" (quoted in Kline, 2015, p. 58). Likewise, in 1953 the engineer Robert Fano, who contributed to information theory, stated that

> I believe, for instance, that expressions for the amount of Information such as those which appear in Shannon's paper can only be used in problems where the transmitter and receiver are well-identifiable, and where one can assume the existence of an ensemble of messages with known statistical characteristics. (Quoted in Kline, 2015, p. 133)

Nonetheless, hundreds of neuroscientists have published calculations of Shannon's information transmitted. Indeed, the use of information theory in various guises is broadening throughout biology (as indicated in the editorials by Milenkovic et al., 2010; Dimitrov, Fekri, Lazar, Moser, & Thomas, 2016). Consider, for example, a series of papers by Giulio Tononi and co-authors (e.g., Tononi, 2008; Tononi, Boly, Massimini, & Koch, 2016), who use an information theory framework to produce what the authors call an *integrated information theory* (IIT) of consciousness. The IIT model itself actually "claims that, at the fundamental level, consciousness is integrated information, and that its quality is given by the informational relationships generated by a complex of elements" (Tononi, 2008, p. 217). IIT has become a topic of popular interest (Reardon, 2019), with the help of some eager publicizing (Zimmer, 2010; Koch & Tononi, 2008, 2017; Koch, 2018). This is hardly the only example of heavy inference being made subsequent to information theory analyses, leading to popular attention. For example, Rolls and co-authors (Tovee, Rolls, Treves, & Bellis, 1993; Tovee & Rolls, 1995; Rolls, Critchley, & Treves, 1996; Rolls, Critchley, Verhagen, & Kadohisa, 2010) have used calculations of information transmitted to support the concept of sparse coding by neurons (Rolls & Treves, 2011), which has become quite trendy (Quian Quiroga, Fried, & Koch, 2013).

The present paper scrutinizes neuroscientists' interpretations of the crucial framework that underlies information theory, namely, the six physical elements that comprise Shannon's general communication system (Shannon, 1948; Shannon & Weaver, 1949). The neuroscientists' interpretations altogether constitute the evidential basis for the present paper. Table 1 (Appendix) presents the aforementioned interpretations. Quotations are sometimes used in the table, in order to illustrate the use of information theory terms in the various author's own words, while minimizing any accusations of inaccuracy or misinterpretation. The cited documents are listed from earliest to most recent, broadly spanning the literature on sensory neuroscience. These documents altogether represent 50 peer-reviewed journals, books, and proceedings, 259 scientists, and more than 113 research institutions (not including cross-appointments). Only English-language literature was surveyed, but this seems to represent the majority of the field.

The total number of neuroscientists who have employed information theory analyses in their publications is unknown. But it is not difficult to find neuroscience laboratories that have produced 20 papers or more that employ information theory analyses, and it is likewise not difficult to find individuals who have co-authored 50 or more such papers. Evidently, it was profitable to do so. Some of those laboratories and some of those individuals are represented in Table 1. One individual, however, is notably absent, namely Kenneth Howard Norwich. Professor Norwich (MD, PhD) emphasized the application of information theory not only to sensory neuroscience but also to sensory psychology, producing so many published documents that the work deserved separate treatment (see Nizami, 2011b). In contrast to all this, some experiment-oriented laboratories produced just one or two published documents that used information theory. Some of those laboratories, too, are represented in the table. Possible reasons for the briefness of their interest are addressed in sections 5–7 (Discussion).

3. Results

Consider first how many of Shannon's six system elements were identified in the neuroscience documents cited here. Warren Weaver set the tone for the neuroscience use of Shannon system elements (Shannon & Weaver, 1949). Weaver alone identified all six Shannon elements. And to Weaver, each Shannon element could be any aspect of a neuron, or of the world around it; no coherent identification emerged. Hagins (1965) and much later McDonnell, Ikeda, and Manton (2011) identified five of the six Shannon elements, although Hagins did not identify the transmitter, and McDonnell, Ikeda, and Manton named the neuron itself as being three of the six elements. Elsewhere, four papers were found naming just four of the six elements (Table 1). Some documents identified none of the six elements (Rapoport & Horvath, 1960; Laughlin, 1981; Tolhurst, 1989; Atick & Redlich, 1990; McClurkin, Optican, Richmond, & Gawne, 1991; Tovee et al., 1993; Gochin, Colombo, Dorfman, Gerstein, & Gross, 1994; Nakao, Kawazoe, & Shimada, 1994; Tovee & Rolls, 1995; Gnadt & Breznen, 1996; Rolls et al., 1996; Buračas, Zador, DeWeese, & Albright, 1998; Sugase, Yamane, Ueno, & Kawano, 1999; Gehr, Komiya, & Eggermont, 2000; Reinagel & Reid, 2000; Borst & Haag, 2001; Nirenberg, Carcieri, Jacobs, & Latham, 2001; Arabzadeh, Panzeri, & Diamond, 2004; Kayser & König, 2004; Matsumoto, Okada, Sugase-Miyamoto, Yamane, & Kawano, 2005; DiCaprio, Billimoria, & Ludwar, 2007; Kumbhani, Nolt, & Palmer, 2007; Gastpar, Gill, Huth, & Theunissen, 2010; Rolls et al., 2010; Suksompong & Berger, 2010; Farfán, Albarracín, & Felice, 2011; Gillespie & Houghton, 2011; Adibi, McDonald, Clifford, & Arabzadeh, 2013; Harvey, Saal, Dammann, & Bensmaia, 2013; Sugase-Miyamoto, Matsumoto, Ohyama, & Kawano, 2014; Witham & Baker, 2015). This trend, of not identifying Shannon's system elements, became commonplace in the 1980s, and became altogether the rule after Rieke and colleagues published an integral-calculus method in the late 1990s (Rieke, Warland, de Ruyter van Steveninck, & Bialek, 1997; Warland, Reinagel, & Meister, 1997; Strong, Koberle, de Ruyter van Steveninck, & Bialek, 1998), a method which was widely adopted in neuroscience (for example, Table 1 entries 46, 49, 54, 58, 61, 65, 66, 70, 73, 79, 82, 83, 84; also Reinagel & Reid, 2000; Borst & Haag, 2001; Nirenberg et al., 2001; Kumbhani et al., 2007; Suksompong & Berger, 2010).

Consider now the identities assigned to individual Shannon system elements. This, too, proves to be illuminating. Begin with destination. This element was ignored in all but four of the documents inspected here, where it is your brain (Shannon & Weaver, 1949, p. 7) or "A detector located at the output of the receiver and operating as a decision-making device like some part of the retina or brain" (Hagins, 1965, p. 405) or "other brain centers" (Heller, Hertz, Kjaer, & Richmond, 1995, p. 176) or "The behavior of the organism that results from the motor signal [that is evoked eventually in response to a stimulus]" (Rathkopf, 2017, p. 322). Of course, the actual destination for the actual information theory calculations is never the brain, as some might assume; rather, it is the laboratory-based investigator, who plays the role of the *observer* (Nizami 2014a, 2014b, 2015, 2017). The role of the observer is a key concept, and it is discussed at length below.

The source was nearly as rarely identified as was the destination. The Shannon element most frequently named was actually the transmitter. Second-most-frequent was the channel, which received so many different interpretations that the reader is referred to Table 1. Although the neuron itself seems intuitively to be a channel, the neuron itself was, ironically, the thing most likely to be identified as the transmitter. Sometimes, a given neuron was deemed both transmitter and channel. A noise source was not often identified, even in the early years; identifications of it dwindled to a trickle after the mid-1970's. Even more remarkably, some of the later documents that identify noise source name no other Shannon system elements (Table 1 entries 12, 24, 27, 35, 54, 75).

Turning now to receiver: this term, too, was not often identified. When named, it could be anything from the next neuron brain-wards (for example, Table 1 entries 32, 46) to some unidentified neuron at the brain (for example, Table 1 entries 39, 58) to the human observer himself (for example, Table 1 entries 4, 19, 38). Note well that the latter case conflates receiver with Shannon's own notion of the destination (Shannon, 1948; Shannon & Weaver, 1949).

4. Interim Summary, and Analysis

Obviously there is a remarkable lack of coherence within neuroscience, both within- and across-studies, over the identities of the elements of the Shannon general communication system. However, in the interests of having an unbiased assessment of the total number of distinct interpretations within each column of Table 1, the present author recruited a doctoral colleague from a different field, unfamiliar with the documents cited in this paper, and encouraged her to choose her own criterion of distinctiveness. She chose a relatively conservative one, under which conceptually-similar interpretations were taken to be identical (such as "we" and "human subjects"; or "uncorrelated principal components [of the spike train]" and "spike counts and spike timing"; or "neuron" and "afferent fiber" and "chemoreceptor"). The resulting number of distinct interpretations of source, transmitter, channel, noise source, and receiver were respectively 10, 23, 12, 15, and 11. This altogether allows 455,400 distinct concatenations of these terms, without even considering the possible interpretations of destination. When the latter are included, there are 1,821,600 potential interpretations of Shannon's general communication system within neuroscience. Of course, a different examiner, holding a different standard of distinctiveness, might arrive at different numbers of distinct interpretations for each column in Table 1. Nonetheless, the total implied number of concatenations of terms would be quite large.

Naturally, not all combinations of Shannon elements will make sense to a particular person. Nonetheless, the above calculations should offer a raw sense of the enormity of the number of available interpretations when engineering labels are assigned willy-nilly to biological phenomena. But we can be even more conservative. Suppose that only 0.1% of the postulated combinations are actually agreeable to all judges. We would nonetheless have 455 unique groupings of source, transmitter, channel, noise source, and receiver, and 1,822 unique groupings of all six of the Shannon elements (i.e., including destination). Such multiplicity represents remarkable incoherence amongst neuroscientists. Factors underlying the gamut are discussed below.

Note well that, in the literature, there are numerous attempts to characterize the neuroscience experiment as a system, which conflate with attempts to describe the neuron itself as a system. This raises an inherent issue, that of scale. The putative whole Shannon system has narrowed over time, from being the organism's environment, including the organism itself (Table 1, entry 1) to being the organism itself (Table 1, entries 1, 3, 4, 14, 38) to being entire sensory subsystems within the organism (Table 1, entries 7, 16, 17, 29, 39, 44, 45, 47, 74) to being chains of neurons (Table 1, entries 13, 58) to being individual neurons (Table 1, entries 8, 22, 25, 83; also Suksompong & Berger, 2010) and finally to being the synapse between individual neurons (see for example Zador, 1998; Manwani & Koch, 2000). The narrower the scope of the study, the fewer (as a rule) were the Shannon system elements identified. Indeed, it is not unthinkable that someone has characterized physiological pathways inside neurons using information-theory calculations. Apparently, the use of information theory in neuroscience is approaching a microscopic vanishing point, insofar as the point of using information theory in neuroscience is progressively vanishing.

Ironically, Tononi raises this issue of the proper scale for information theory calculations, in an attempt to justify his own integrated information theory:

> An outstanding issue is finding a principled way to determine the proper spatial and temporal scale to measure informational relationships and integrated information. What are the elements upon which probability distributions of states are to be evaluated? For example, are they minicolumns or neurons? And what about molecules, atoms, or subatomic particles? Similarly, what is the "clock" to use to identify system states? Does it run in seconds, hundreds of milliseconds, milliseconds, or microseconds? (Tononi, 2008, p. 234)

In these few lines, Tononi inadvertently identifies much of what is wrong with any attempt to understand neuronal firing through information theory. This topic will be expanded below, within the context of examining three things that influence the gamut in Table 1: the ignorance of the role of the observer, the notion of decoding (which is inseparable from the notion of the observer), and the pursuit of inappropriate metaphors.

5. Discussion: The Role of the Observer in Calculating "Information"

5.1 Tononi's Integrated Information Theory (IIT): What Came First, the Consciousness or the Observer?

In the Introduction, it was noted that the use of information theory is broadening throughout biology. Dr. Giulio Tononi and his co-authors were given special mention, because they use an information theory framework to produce their IIT of consciousness. That theory deserves further scrutiny. That scrutiny reanimates a concept that is crucial within second-order cybernetics, namely, the role of the observer.

But let us begin not with Tononi but with Christof Koch, a long-term contributor to IIT (Tononi & Koch, 2008, 2015; Koch, Massimini, Boly, & Tononi, 2016; Tononi et al., 2016). Indeed, Koch (2012) touts IIT in his book *Consciousness: Confessions of a Romantic Reductionist*. The book was reviewed by the senior philosophy professor John Searle (Searle, 2013). Searle notes that "no reason has been given at all why there should be any special connection between information theory and consciousness" (Searle, non-numbered page). Searle states that

> Consciousness is independent of an observer. I am conscious no matter what anybody thinks. But information is typically relative to observers. These sentences, for example, contain information that make sense only relative to our capacity to interpret them. So you can't explain consciousness by saying it consists of information, because information only exists relative to consciousness. (Searle, 2013; n.p.)

Note that "consciousness is independent of an observer" is an assumption. Also, Searle momentarily conflates information that carries meaning (in the commonsense notion of information: "Which street leads to Chester?") with the Shannon notion of information, as a statistic within the narrowly circumscribed model described by Shannon. Nonetheless, in information theory an observer is needed, in order to calculate information transmitted (or other related measures), although Shannon does not say so (Nizami, 2015). Particularly, the observer is required to know the probabilities of particular symbols (see Introduction).

Regardless, Searle (2013) makes a crucial point: that consciousness precedes and is necessary for information, not the converse, no matter what is meant by *information*. In other words, consciousness is needed to calculate any information statistic, such as the ones that, according to Tononi et al., allegedly define consciousness. In short, Tononi and Koch and their various co-authors (citations above) have reversed the normal cause-and-effect. Remarkably, such a reversal had been proposed three decades earlier, in an extraordinarily similar theory, K. H. Norwich's entropy theory of perception (e.g., Norwich, 1993). That model is permeated by an unanswered, nagging question, namely, "What came first, information accrual or perception?" (Nizami, 2010b). There is a correct answer, which is perception (Nizami 2009a, 2009b, 2010b), where we can momentarily take *perception* to be interchangeable with *consciousness*, following a tradition that dates back to Patrick (1922, p. 704) and perhaps earlier.

Tononi and his various colleagues commit yet another error. They employ information theory to infer content—for example, not only how well a symbol's or whole message's destination probability matches its source probability, but what the symbol or whole message means. This, too, occurs throughout Norwich and colleagues' entropy theory, in which Shannon's information transmitted, described by Shannon as reduction of uncertainty (Shannon & Weaver, 1949), is habitually interpreted as gain of information, where information is taken to be knowledge and knowledge is taken to be something meaningful. But, as Searle (2013, non-numbered page) correctly reminds us, "The *mathematical theory of information* is not about content" (italics added).

Regarding again Tononi's IIT, Searle says that "Tononi and Koch want to use both types of information, they want consciousness to have content, but they want it to be *measurable* using the mathematics of information theory" (Searle, 2013, non-numbered page; italics added). And Searle is right; consider, for example, Tononi's statement that

> The *quality* of consciousness is determined by the set of all the informational relationships its mechanisms generate. That is, how integrated information is generated within a complex determines not only the amount of consciousness it has, but also *what kind* of consciousness. (Tononi, 2008, p. 224; italics added)

In response to Searle (2013), Koch and Tononi were allowed a reply, accompanied by a rebuttal by Searle (cited here as Koch, Tononi, & Searle, 2013). Koch and Tononi state that "IIT introduces a novel, non-Shannonian notion of information—integrated information—which can be measured as 'differences that make a difference' to a system from its intrinsic perspective, not relative to an observer" (Koch et al., 2013, n.p.). By "differences that make a difference," Koch and Tononi presumably refer to Bateson's (1972) statement that "In fact, what we mean by information—the elementary unit of information—is a *difference which makes a difference*, and it is able to make a difference because the neural pathways along which it travels and is continually transformed are themselves provided with energy" (Bateson, p. 459; original italics). But here Bateson himself may be conflating the *bit* of information theory with the notion of information as something meaningful. (Readers are invited to judge for themselves.) Regardless, the adjoining idea that IIT uses non-Shannonian information seems untrue, as a glance at the mathematics of IIT will reveal. Equally absurd is the system's alleged "intrinsic perspective, not relative to an observer." Both of these points will be discussed below. Searle's rejoinder (Koch, Tononi, & Searle, 2013) repeats his criticisms and points out that Koch and Tononi had not actually answered them.

Cerullo had already firmly rebutted Tononi:

> There is no current understanding of how to develop a mathematical or computational model of meaning (if this is even possible) ... IIT illustrates the limitations of abstract theories of consciousness [that are] generated without taking the architecture of the one system we know generates conscious experience, the brain, into account. (Cerullo, 2011, p. 57)

In other words, Tononi and co-authors propose to explain consciousness without explaining its underlying mechanisms, beyond simply claiming that mechanisms generate informational relationships. Tononi and colleagues assume that informational relationships cause consciousness rather than merely correlating with it. But even emergent phenomena (Nizami, 2017, 2018) require underlying mechanisms; we will return to this issue below. Meanwhile, note well that a recent survey (Michel et al., 2018) suggests that those scientists who accept IIT may be relatively lacking in research expertise in precisely the subject that IIT purports to explain, namely, consciousness.

5.2 The Observer, All-Knowing

Shannon's general communication system is symmetric; it contains an encoder, the transmitter, and a decoder, the receiver. Figure 3 schematizes this symmetry, which was present in Fig. 1, and also introduces a feature not shown in Fig. 1, as follows. As described in the Introduction, the receiver converts the noisy signal back into a message, a message containing some subset of the symbols that were originally available to form it at the source. The message is passed to a destination, who is presumably a human being. But information transmitted is calculated by yet another personage, the observer (Nizami, 2015, 2017). The observer must perforce be all-knowing, because the observer knows all of the possible inputs to the general communication system, as well as their Shannon probabilities (see Introduction). The observer also knows all of the actual inputs and outputs. Remarkably, Shannon himself omitted the observer, as noted by a champion of second-order cybernetics, Ranulph Glanville. Glanville recognized that the observer is "in the system and is taking part" (Glanville, 2007, p. 388). Glanville also noted two implicit assumptions about the general communication system: that the meaning of a message "is perfectly mapped onto" the message (Glanville, p. 377), and that "the meaning at one end is the same as that at the other" (Glanville, p. 377). In short, there is a shared set of understandings between the sender (the source) and the recipient (the destination). Not only may the sender build meaning(s) into a message that is to be transmitted, but the recipient may attempt to derive meaning(s) from whatever is then received. In contrast, the observer works with probabilities in order to calculate information transmitted, and need not, in principle, understand the messages at all. Shannon's information transmitted is a measure of fidelity of data transfer (specifically, how well probabilities of presentation are preserved at the receiver), not a measure of "meaning transfer." Indeed, messages can even be encrypted, or otherwise composed in an unfamiliar language.

In laboratory experiments, the neuroscientist becomes the observer. The neuroscientist remains unchanged (to a convenient first approximation) when examining a research organism's response to sensory stimuli and subsequently using those responses to calculate information transmitted, according to a method described below. However, unlike the neuroscientist, the research organism itself "is changed by their interaction with the stimulus. The stimulus is 'a difference that makes a difference'" (Nizami, 2011b, p. 1111). Even if the organism is not alert, or is in fact asleep, these points remain true. Consider that if neurons in an anesthetized or sleeping organism nonetheless fire spikes to a sensory stimulus, then repeating that same stimulus can evoke different, and (on average) usually lesser, numbers of spikes over time. This phenomenon is well-known and is called firing-rate adaptation; Nizami (2010b) discusses some examples.

5.3 The Observer as Homunculus

Nizami (2015, 2017) has detailed the role of the observer in observing voltage-spike trains and in using them to perform information-theory calculations. The de facto observers of neurons are the laboratory staff (Nizami, 2015, 2017). But there is an absurd (and popular) interpretation that is implied in the literature, namely, that the observer resides within the experimental research subject, whether that subject is human or non-human, in the form of a homunculus—in fact, as an infinite regression of homunculi (explained in Nizami, 2009a, 2015, 2018). For example, Tononi and his colleagues rely on information-related statistics, but their reliance implies the existence of a homunculus to calculate those statistics—inevitably, an infinite regression of such homunculi. Perhaps not surprisingly, the same infinity of homunculi is found within K. H. Norwich's entropy theory of perception (see Nizami, 2009a, 2009b, 2010a, 2010b, 2011b), within which consciousness (as perception) allegedly derives from differences in Shannon information.

Recall Searle's (2013) comments about IIT (above). Recall also the declaration by Koch and Tononi (in Koch et al., 2013, non-numbered page) that "IIT introduces a novel, non-Shannonian notion of information—integrated information—which can be measured as 'differences that make a difference' to a system from its intrinsic perspective, not relative to an observer." This was to be repeated in Tononi et al. (2016, p. 457): "In IIT, information is causal and intrinsic: it is assessed from the intrinsic perspective of a system based on how its mechanisms and present state affect the probability of its own past and future states (cause–effect power)." Aside from asking how one might affect the probability of a past state, let us note well the system's alleged "intrinsic perspective" (Koch & Tononi in Koch et al., 2013; Tononi et al., 2016). This seems to suggest that neurons are self-observing; more will be said on this below. As Tononi et al. (2016, p. 457) continue: "By contrast, Shannon information is observational and extrinsic—it is assessed from the extrinsic perspective of an observer and it quantifies how accurately input signals can be decoded from the output signals transmitted across a noisy channel." Let us critically examine these statements. First, the information of IIT is unquestionably some interpretation of Shannon information theory. Therefore, Tononi et al.'s first statement contradicts their second statement. Mørch (2019), for one, recognizes that the information in IIT is indeed extrinsic, in contrast to consciousness itself, whose "intrinsic property is a property that does not constitutively depend (though it may well causally depend) on properties of other things, or its external surroundings" (Mørch, p. 133). The "intrinsic perspective" of Tononi and colleagues (Koch and Tononi in Koch et al., 2013; Tononi et al., 2016) requires a homunculus—in fact, an infinite regression of homunculi.

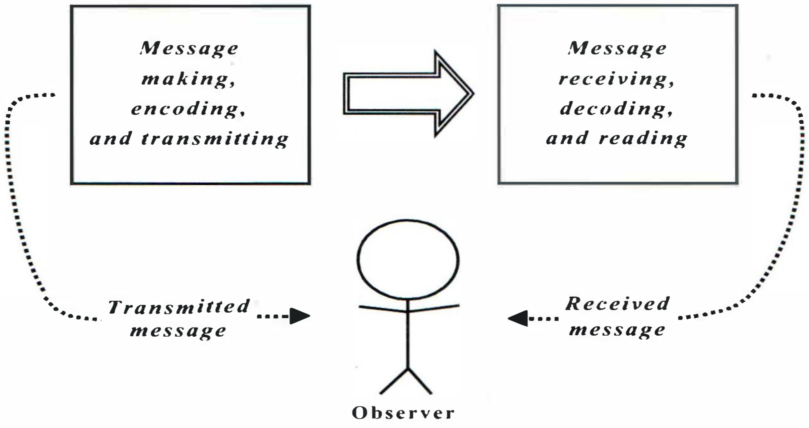

Figure 3. The mirror-image structure of the Shannon general communication system. Calculating information transmitted requires the observer. The observer is required to know both the transmitted message and the received message, hence the dotted lines that both lead to the observer.

6. Discussion: Decoding, in which the Neuron is the Observer

6.1 The Neuron as the Observer

Remarkably, the sensory-neuroscience literature not only implies but sometimes actually specifies that neurons themselves are observers of other neurons (Nizami, 2015, 2017). For example, the observer may appear in the literature as the receiver/ detector. Reinagel, Godwin, Sherman, and Koch (1999, p. 2559) encapsulate the alleged relation of observer to information to receiver as follows: "The 'information' in a neural response is defined as the extent to which observing the response would reduce a receiver's uncertainty about the particular visual stimulus." But here Reinagel et al. conflate the Shannon notion of receiver with that of an observer who stands apart from the receiver-containing general communication system. Reinagel et al.'s observer/receiver is assigned no firm identity. Reinagel et al. imply that it must be a neuron. All of this is typical of the neuroscience literature. Observer-neurons "read" spike trains emanating from other neurons, in order to decode those spike trains. Decoding then allegedly allows the observer to reconstruct or estimate the actual sensory stimulus (Nizami, 2014b, 2017).

The ubiquitous presumption of neurons as observers dates back at least to the attempt by Lettvin, Maturana, McCulloch, and Pitts (1959) to explain what the frog's eye tells the frog's brain, in which consciousness was effectively granted to individual neurons (Nizami, 2017). Going beyond Lettvin et al., we can rhetorically ask how else, besides having individually conscious neurons, could an animal's consciousness arise? And how could neurons be individually conscious, unless ... unless everything that composed a neuron was (hypothetically) conscious! Nizami (2017, 2018) offers an alternative to this downward spiral to smaller and smaller conscious constituents, namely, *emergence.* In this phenomenon, "Consciousness emerges from the activity of vast numbers of interacting neurons. Likewise, from vast numbers of interacting consciousnesses emerge societies, whether animal or human. One part of human society is the laboratory group, containing the neuroscientist" (Nizami, 2017, p. 1520). Certainly, it is the laboratory group, not the neuron, who perform observations and any subsequent decoding (Nizami, 2015, 2017).

The neuroscience version of the Shannon general communication system is non-symmetric. Figure 4 illustrates this asymmetry. Note well that the right-hand-side of the general communication system (Fig. 1) is now encapsulated within homunculus, which may explain the very few, and very different, accounts of receiver and destination in the neuroscience literature.

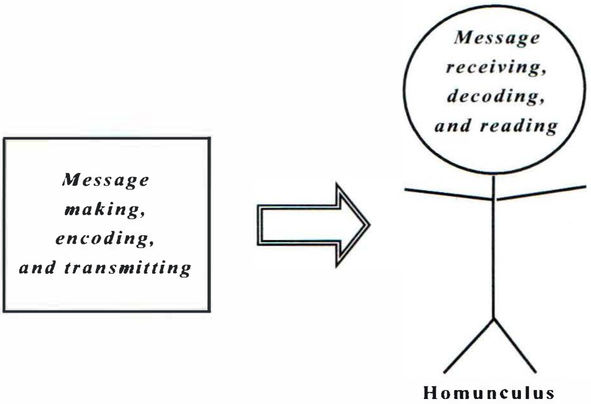

Figure 4. The Shannon general communication system in neuroscience experiments. Compare to Fig. 3. The observer is now the homunculus, which cannot know the stimuli applied by the laboratory experimenter; it can only know the organism's neuronal responses. Information-transmitted calculations are actually done by the laboratory experimenter, who knows both the sensory stimuli and the organism's neuronal responses—the transmitted message and the received message (Fig. 3).

6.2 The Neuroscientists' Confusion Matrix

Recall the original Shannon confusion matrix (Fig. 2). It contains the numbers needed to calculate information transmitted. And furthermore, it is square; the number of rows equals the number of columns. Now consider the neuroscience version. Figure 5 illustrates the neuroscience confusion matrix. This particular one is square, but only for simplicity of comparison to Fig. 2; in the literature, square versions are rare (Nizami, 2014b). Note that the neuroscientists' symbols sent (events) are the applied sensory stimuli, so that the matrix's columns are labelled by stimuli—or perhaps by stimulus ranges, called *stimulus categories*. This difference arises because a stimulus feature such as intensity forms a continuum, at least to our measuring instruments. However, the stimulus could be a unitary thing, that is, a Gestalt, such as a face. Even so, a face can change along any number of dimensions, perhaps indiscriminably to the human eye. Note also the neuroscientists' symbols received (outcomes). These are typically the numbers of stimulus-evoked voltage spikes, as counted over some spike-counting time. But, as noted above, voltage-spike production is stochastic; repeating the stimulus may produce a different spike-count. Altogether, then, the confusion matrix's rows represent *spike-count categories*.

Customarily, a stimulus category k contains just one face or just one intensity. But the reasons for this are not explained in the literature. Hence, consider the following rationale. If different stimuli within a single stimulus category consistently evoke spike-counts that fall within different spike-count categories, then each of the differing stimuli can effectively be placed within a separate stimulus category. Conversely, if m different stimuli within the particular stimulus category are sufficiently similar that the resulting spike counts fall within just one spike-count category, then those *m* different stimuli are imitating a single stimulus repeated *m* times. These issues confuse the very interpretation of I_t. In practical attempts at clarification, each stimulus category is operationally restricted to a single stimulus, which differs sufficiently from all the others employed, such that the difference between stimulus and stimulus category effectively disappears.

6.3 Decoding, Sometimes Called Reconstruction: The Underlying Rationale

In a typical neuroscience confusion matrix, each matrix entry is the number of times that a particular stimulus evokes a spike count that falls within the particular spike-count category. In terms of the equations in the Introduction, $p(k)=N_{.k}/N$ is now "the probability of giving stimulus *k*," and $p_j(k)=N_{jk}/N_{j.}$ is now "the probability that stimulus *k* was given, for a particular spike count in spike-count category *j*." However, and in contrast to the calculations explained in the Introduction, obtaining I_t now requires a further step by the experimenter, a step assumed to be carried-out by some neuron: namely, to work backwards from each stimulus-evoked spike count so as to infer (in practicality, based on a recorded distribution of spike counts) what stimulus is implied to have been given. Such inference, called decoding or *reconstruction*, has been attempted numerous times in the literature (for instructional examples, see Georgopoulos & Massey, 1988; Furukawa & Middlebrooks, 2002).

Decoding is a focus of the review paper "Neural Coding: Computational and Biophysical Perspectives" (Kreiman, 2004). Kreiman concerns himself with coding by neurons and with decoding (within the animal) of the coded messages. In so doing, Kreiman reinforces the contemporary state of thinking about neurons, including their anthropomorphization (Nizami, 2017). For example, Kreiman (2004) writes of "encoding of information in the nervous system" (p. 73), "neuronal communication" (p. 73), "bits conveyed by neurons about sensory stimuli" (p. 74), and neurons carrying messages. He even speaks of neurons reading, of being interested, of caring, of listening, and of talking, as readers can confirm for themselves. Note well that the neuron already has many human manifestations in the greater literature (Nizami, 2017); to that list we must now add psychotherapist.

Kreiman (2004) rationalizes decoding. In so doing, he perpetuates a cardinal error common to the neuroscience literature, namely, the vague and over-frequent use of the engineering terms *signal* and *noise*. Consider the following:

> Embedded in the idea of a code is the notion that some aspects of neuronal activity can be discriminated as a signal while other aspects may be due to noise. The distinction between what constitutes a signal and what constitutes noise will be a fundamental one. (Kreiman, 2004, p. 73)

	Stimulus category						
	1	**2**	**-**	**k**	**-**	**n**	**Row totals**
Spike-count category							
1	N_{11}	N_{12}	-	N_{1k}	-	N_{1n}	$N_{1.}$
2	N_{21}	N_{22}	-	N_{2k}	-	N_{2n}	$N_{2.}$
-	-	-	-	-	-	-	-
j	N_{j1}	N_{j2}	-	N_{jk}	-	N_{jn}	$N_{j.}$
-	-	-	-	-	-	-	-
n	N_{n1}	N_{n2}	-	N_{nk}	-	N_{nn}	$N_{n.}$
Column totals	$N_{.1}$	$N_{.2}$	-	$N_{.k}$	-	$N_{.n}$	**Sum** $= N$

Figure 5. The Confusion Matrix of Sensory Neuroscience.

Fundamental indeed, insofar as being meaningless. That is, neural spike-firing variability is typically cast as representing neuronal noise. This renders impossible any identification of neuronal signal in terms of that selfsame spike-firing.

There is more. Note well Kreiman's (2004, p. 74) question, "What would it mean to understand the neural code? We would like to be able to predict the neuronal activity from a given stimulus and guess which stimulus was presented based on the neuronal activity." The reasons for guessing the stimulus appear much later in Kreiman's paper, where Kreiman describes the sensory neuronal responses to a moving object which is being seen by the organism, responses that evoke an eventual avoidance maneuver, as when the fly takes flight to avoid the looming fly-swatter:

> These codes need to be decoded to ultimately exert any effects on behavior. At the processing stages near the motor output, the decoders can be the muscle cells themselves. Muscle cells have to interpret the commands by the pre-synaptic neurons and transform those into appropriate behavior. For other processing stages more remote from the output, a set of post-synaptic neurons is in charge of decoding and recoding. (Kreiman, 2004, p. 90)

Note the words *behavior*, *interpret*, *commands*, and *in charge*, all of which might characterize a homunculus. Unquestionably, the homunculus is the metaphor underlying decoding (Nizami 2014b, 2015, 2017).

The literature contains many purpose-built algorithms for decoding (noted in Nizami, 2014b, 2015, 2017). All such algorithms are assumption-laden mathematical models, that are tantamount to guesswork—hence Kreiman's (2004) use of the word *guess*. To decode with certainty would require knowing the neuronal code for the stimulus property (such as intensity) that is manipulated by the experimenter. And here we confront the crux of the matter: The putative neuronal code is unknown, perhaps unknowable (Nizami, 2014b, 2017). Consider that not even an appropriate interval for counting spikes can be declared, because there is no firm context for the notion of "appropriate" (Nizami, 2019)! And indeed, rather than averaging voltage-spike counts over counting times, some researchers have attempted to quantify spike-firing rates as instantaneous. Here, too, there are problems; there are different ways of quantifying instantaneous, with no clarity as to which quantification should be employed. All of this is explained by Lansky, Rodriguez, and Sacerdote (2004) and their predecessors cited therein, within one particular context, that of the calculable but unnatural case of stationary spike firing, in which the underlying stochasticity is unchanging over time (i.e., no adaptation).

In a crushing irony, the very same reason that Shannon's information theory was applied to neurons in the first place—namely, the stochastic firing of voltage spikes in response to a sensory stimulus—renders impossible a correct calculation of information transmitted. Spike-firing variability is cast by neuroscientists as Shannon's noise; but Shannon's own noise is really a second signal, its hypothetical origin a noise source (Fig. 1). It is a signal that acts to corrupt the symbols sent (Fig. 1). Those symbols have their own inherent randomness, as reflected by their a priori probabilities (Introduction). But the latter variability is distinct from the stochasticity of voltage-spike firing, which in turn is distinct from Shannon's independent additive noise. Furthermore, casting the neural spike-firing variability as representing neuronal noise makes it impossible to identify neuronal signal in terms of that selfsame spike-firing. Altogether, these distinctions explain the uncoordinated plethora of interpretations of noise source in Table 1.

6.4 The Fallacy of Models as Predictors

Notwithstanding the impossibility of the neuroscientists' decoding, I_t has been used in the literature to tout some putative neuronal codes as being superior to others. For example, spike count has been compared to first-spike latency, principal components, and so forth (briefly reviewed in Nizami, 2014b). But it is entirely fallacious to assume that Shannon information theory can identify which alleged neuronal code is the actual one, even assuming that such a code exists. To assume a neuronal code is an anthropomorphic assumption. Secondly, codes are assumed to convey meanings. However, as noted above, information theory does not gauge meanings. Meaning is created by a mind, and is exchanged with other minds. The mind itself presumably emerges from mechanoelectrical mechanisms. Altogether, it seems that meaning requires mechanisms; this remains true even if messages arising from mechanisms are encrypted and hence are seemingly (at first glance) meaningless. However, information theory is independent of mechanism (Nizami, 2008), insofar as it neither discovers nor dictates mechanisms. That is, although Shannon's information theory depends upon the general communication system, it nonetheless neither discovers nor dictates the actual mechanisms of transmission or reception or symbol genesis or noise genesis. Such processes merely exist independently; that is, information theory ignores context, insofar as information theory cannot specify exactly how a transmitter is built (for example), or how data are generated at the source. Truly, Shannon information theory cannot discern mechanisms, because it is merely a model, and no model whatsoever can discern mechanisms. As such, Shannon information theory cannot discern meaning, because meaning requires context, and context is not independent of mechanism. Note well that even though meaning requires context, context itself (for example, available choices of messages at a source) does not require meaning.

If all this is unclear, consider another approach to the issue: how models are built. Once a set of empirical observations are obtained, one or more assumptions are postulated, from which a conceptual model is crafted. From the conceptual model, a mathematical model might arise. Regardless, with the data having typically been followed by one or more assumptions, all the sorts of models that eventually derive from those assumptions are themselves tantamount to assumptions. Shannon's general communication system is a physical construct which itself represents a set of assumptions. But assumptions do not constitute explanations. This distinction is profound. Phrased yet another way, models are not predictive. No model predicts the existence of gravity, or of matter, or of energy. No model dictates mechanisms; models only produce possibilities. By the same token, no mathematical model is independent of its grounding, namely, its conceptual framework of assumptions. Nonetheless, neuroscientists have taken Shannon's man-made general communication system, a framework of assumptions which is the grounding for Shannon's algebra, and have supplanted it by neuronal "communication systems" of arbitrary content (Table 1). In so doing, they have been pushing a gratuitous analogy, the analogy of neurons as communication systems.

7. Discussion: Analogy

7.1 Warren Weaver and the Communication Metaphor

The use of information theory grew and persisted outside of engineering. One might marvel at this. In fact, Shannon (1956), Wiener (1956), and others (for example, Elias, 1958; Johnson, 1970) had expressed exasperation early-on about non-engineering uses of information theory. Ironically, the ultimate blame can be placed squarely upon Warren Weaver's opening chapter in Shannon and Weaver (1949), wherein he used analogies freely. Any apparent similarity was taken by Weaver to indicate equality, in a trend that was soon to be emulated by many others (documented in Kline, 2015). Consider Weaver's interpretation of a Shannon channel and its associated phenomena:

> In the case of telephony, the channel is a wire, the signal a varying electrical current on this wire; the transmitter is the set of devices (telephone transmitter, etc.) which change the sound pressure of the voice into the varying electrical current. In telegraphy, the transmitter codes written words into sequences of interrupted currents of varying lengths (dots, dashes, spaces). In oral speech, the information source is the brain, the transmitter is the voice mechanism producing the varying sound pressure (the signal) which is transmitted through the air (the channel). In radio, the channel is

> simply space (or the aether, if anyone still prefers that antiquated and misleading word), and the signal is the electromagnetic wave which is transmitted. (Shannon & Weaver, 1949, p. 7)

In short, the source, the transmitter, the channel, and the symbols sent (signal) are whatever Weaver wants them to be, independent of the receiver. Such indulgence was soon to be repeated elsewhere (Moles, 1966, as recounted in Nizami, 2011b). Those interpretations set a lax standard for what followed in neuroscience. Note Weaver's attitude to a key Shannon concept, symbol: "This is a theory so general that one does not need to say what kinds of symbols are being considered—whether written letters or words, or musical notes, or spoken words, or symphonic music, or pictures" (Shannon & Weaver, 1949, p. 25). Or (scant years later) sensory stimuli applied to a laboratory animal. Weaver continues: "The theory is deep enough so that the relationships it reveals *indiscriminately apply to all these and to other forms of communication*" (Shannon & Weaver, p. 25; italics added). Neuroscientists took all this to mean that "Information theory provides a natural framework to study communication in most systems, and the brain is no exception" (Ince, Petersen, Swan, & Panzeri, 2009, p. 13). Communication was to be any form of interaction whatsoever; according to neuroscientists, one such interaction is the continuation of voltage spikes from one neuron to another by means of inter-neuronal synapses (Table 1).

The analogy of the Shannon general communication system as any so-called communication system has propagated widely and deeply. Some truly amusing examples, both new and old, are available. Consider Mathijssen, Culver, Bhamla, and Prakash (2019), who describe a 1-mm-long species of unicellular organism called a protist, which can live in water, forming cellular communities. This particular kind of protist can rapidly contract its body, creating a pressure wave that provokes others in its community to likewise contract, in a chain reaction. Mathijssen et al. (p. 560) refer to this chain reaction as communication, with the protist's contraction itself named as the transmitter and the responding cells named as the receivers (Mathijssen et al., p. 560). Mathijssen et al. (p. 560) also allude to biological signals and noise. Their interpretation of information transmission has already entered the mainstream as a featured article in *Physics Today* (Berkowitz, 2019), the magazine of the American Institute of Physics, whose 10 member-societies altogether include more than 100,000 people.

As an older example, consider a paper of Harvard Professor Edward O. Wilson, the two-time Pulitzer Prize-winning author of popular-science books. Wilson (1962) evaluated "the amount of information in single odour trails" that are extruded as guides by fire ants "as they pertain to the location of the food find" that has been discovered by the ant in question (Wilson, p. 148). According to Wilson, the so-called information is "presented by the trail and transmitted to the follower workers" (Wilson, p. 148), i.e. to the other worker ants who will benefit from the food. Wilson actually calculates the signal uncertainty/information I_S as the "source entropy" of odor trails and I_t as the "information transmitted between individual workers" (Wilson, p. 153).

7.2 The Map Versus the Territory: The Problem of Ingrained Analogy

The analogy of neurons (and other biological features) as communication systems has been remarkably persistent. Why? Sullivan-Clarke (2019), a sociologist, indirectly answers the question through a study of the persistence of metaphors in general. Sullivan-Clarke explains,

> Metaphors are a social product of a historically situated community, and often scientists draw from everyday language in order to address their epistemic needs. When doing so, scientists run the risk of importing implicit assumptions and/or biases of the metaphor into their practice. (Sullivan-Clarke, 2019, p. 154)

One such element of everyday language is the word *information.* Sullivan-Clarke explains that the bias continues as scientists "discover" data that suits the metaphor and neglect data that does not (the phenomenon of confirmation bias).

Sullivan-Clarke explains that metaphor-driven research uses analogies:

> Initially, scientists make a comparison between two analogues: the target analogue and the source analogue. The target analogue is the phenomenon currently under investigation; it is less familiar. In contrast, the source analogue is something that is more familiar or better understood. For example, scientists may appeal to waves in the water as a source analogue in order to hypothesize about sound waves (target analogue), or they may use the sexual behavior of guinea pigs as a source analogue to learn more about human sexual behavior (target analogue). (Sullivan-Clarke, 2019, p. 156)

Unfortunately, as Sullivan-Clarke notes (p. 160), it is possible that "the metaphor becomes commonplace to the point that its use is no longer recognized as metaphorical." In other words, *the map is mistaken for the territory that it describes.* But the map is most emphatically not the territory (Korzybski, 1933; after Bell, 1933).

As a way to avoid ingrained analogies, Sullivan-Clarke offers a suggestion from Turbayne (1962). That is, Turbayne "proposes testing the analogies of a community's metaphor by contrasting it with those of a competitor" (Sullivan-Clarke, 2019, p. 161), because "A competing metaphor provides a different filter for looking at the world" (Sullivan-Clarke, p. 161). But, as Sullivan-Clarke warns us, in a passage that is ironically appropriate for neuroscientists who use information theory,

> Communities that are homogeneous—ones whose members have similar backgrounds and practical experiences—will lack the resources to achieve a robust critique capable of destabilizing an ingrained analogy because individual members may have little to offer in critiquing the assumptions that ground a community-endorsed metaphor. (Sullivan-Clarke, 2019, p. 163)

In other words, neuroscientists are not equipped to criticize those scientists, typically physics-trained, who derived information-transmission integrals and who subsequently wrote the integral-evaluating software (for a description of some of that software, see Goldberg, Victor, Gardner, & Gardner, 2009; Ince, Mazzoni, Petersen, & Panzeri, 2010; Effenberger, 2013; Cessac et al., 2017).

7.3 An Ingrained Analogy: Neural Networks as Networks of Actual Neurons

In a further irony, an inadvertent example of ingrained analogy appears in a recent critique of Tononi's IIT. That is, Doerig, Schurger, Hess, and Herzog (2019) note that, according to IIT, no consciousness is evoked by the feedforward sweep of stimulus-evoked neuronal spikes, but that consciousness does arise when there is consequent top-down activation of those same neurons, in the phenomenon of recurrent processing. Doerig et al. (2019) pursue these notions within the context of neural-network models:

> Both recurrent networks and multilayer feedforward networks are universal function approximators. That is, they can be used to generate any desired input-output function to any degree of accuracy using a finite number of neurons. Therefore, for any recurrent network with a given input-output behaviour, there are corresponding feedforward networks with the same characteristics (although feedforward networks often need many more neurons than their recurrent counterparts). (Doerig et al., 2019, p. 51)

For the moment, let us ignore just how recurrent networks might manifest, given that all neurons are believed to be one-way spike carriers. Doerig et al. (2019, p. 52) declare that "any behavioural experiment can be seen as an input-output function," that is, the experiment can be described by neural-network models. In principle, not just one model, but a potentially infinite number of them. Note well that by behavioural experiment, Doerig et al. refer to an experiment that requires subjective reports from participants. Altogether, Doerig et al. (2019) imply that any behavioral experiment can be described by either feedforward networks or recurrent networks. But, according to Doerig et al., IIT requires recurrent networks for consciousness, and therefore IIT cannot be correct.

But there is a problem. Although IIT is unquestionably fatally flawed (see section 5), Doerig et al. (2019) have nonetheless mistaken the map for the territory. A neural-network model is not an actual network of neurons; the latter would involve far-more-elaborate connectivity than any present-day model could bear. As Searle (1994, pp. 212–225) reminds us, a model of a neurophysiological process is not a neurophysiological process, and as such it need not reveal anything about such a process (no model can discern mechanisms). Nonetheless, Doerig et al. (2019) effectively assume that a mathematical-network model that grossly oversimplifies Nature can be conscious, regardless. Their attitude seems to reflect an ingrained analogy: If it acts conscious, then it is conscious. Of course, another thing that acts conscious (to some onlookers) is one of the psychiatrist Grey Walter's famous *tortoises*, that are primitive robots (Walter, 1950; Holland, 2003). But no psychiatrist, including Grey Walter himself, would call them conscious.

7.4 A Persistent Metaphor: Nature as Trivial Machine

There is an ubiquitous and relevant metaphor in the life sciences that Sullivan-Clarke (2019) mentions but does not pursue, namely, nature as machine. Nicholson (2019), however, does indeed pursue this metaphor, and at length. Nicholson asks, "Is the cell really a machine?" Nicholson (p. 108), a biologist, notes that "The main interpretive framework in molecular biology is *mechanicism*" (original italics). He explains further:

> Modern proponents of mechanicism conceive of the cell as an intricate piece of machinery whose organization reflects a pre-existing design, whose structure is wholly intelligible in reductionistic terms, and whose operation is governed by deterministic laws, rendering its behaviour predictable and controllable—at least in principle. (Nicholson, 2019, p. 108)

Nicholson calls the dominant molecular-biology paradigm the *machine conception of the cell* (MCC). One such cell, of course, is the neuron.

Now, second-order cybernetics is concerned with machines of various kinds (von Foerster, 1984, 2003). Regarding machines, Nicholson notes that

> Machine analogies and metaphorical references to 'locks', 'keys', 'gates', 'pumps', 'motors', and 'engines' continue to pervade the technical literature, as does talk of the 'machinery' and 'circuitry' that underlies the cellular organization. The MCC itself is seldom explicitly defended; it has become so engrained [*sic*] in our minds that we simply take it for granted. (Nicholson, 2019, p. 109)

This is the problem of ingrained analogy that Sullivan-Clarke (2019) decries. To understand the machine analogy, let us first heed Nicolson's own account of machine:

> Although there are many different kinds of machines, a machine can be characterized in very general terms as a device with fixed interacting parts that operate in a coordinated fashion to produce a predetermined outcome. More specifically, one can identify four distinctive properties of machines that are particularly relevant in contemporary formulations of the MCC. First, machines can be described in terms of a list of parts and a blueprint indicating how those parts fit together, meaning that someone who has never seen a particular kind of machine should in principle be able to assemble any number of copies—each virtually identical in appearance and performance—provided they can consult the machine's design specifications. Second, as machines are designed to perform highly specific functions, their operation is tightly constrained, which is why it is possible to predict and control their behaviour. Third, machines are highly efficient in what they do because they always follow the exact same sequence of steps in every cycle of their operation. And fourth, the operation of machines is not continuous; their functioning can be interrupted and their parts examined without thereby jeopardizing their structural integrity. (Nicholson, 2019, p. 109)

This is the familiar *trivial machine* of Heinz von Foerster (von Foerster, 1984, 2003), although Nicholson does not use those terms. But why use machine metaphors in the first place? Nicholson (2019, p. 120) explains: "Just as cars manufactured in an assembly line according to the same model design will behave almost identically, cells endowed with the same genetic program and grown in the same conditions are expected to behave almost identically."

7.5 An Alternative Metaphor: Nature as Non-Trivial Machine

The metaphor of cell as machine contains a sub-metaphor, cell as containing circuits, or being parts of circuits. That is, as Nicholson (2019, p. 115) observes, there is "the widespread appeal to wiring diagrams and design charts (akin to those found in mechanical and electronic engineering) in schematic representations of metabolic, regulatory, and signalling pathways." Signaling pathways—such as the physical pathways carrying sensory input to (and within) the brain, or the actual transformations that occur along those paths.

The concept of pathway is a core analogy that underlies the life-sciences literature. This is one thing that Nicholson (2019) does not emphasize strongly enough. A sequence of biological processes linking a starting scenario to an eventual outcome is mapped as an actual physical sequence of steps between two geographic places. Biological activity has now become the flowchart or the circuit diagram. The territory has become the map. But Nicholson, after performing an extensive review of cellular anatomy and physiology, concludes that

> Cells lack all four characteristic properties of machines that were identified in the introduction. First, once the crucial role that self-organization plays in shaping the cellular architecture is acknowledged, it is difficult to uphold the idea that the spatiotemporal arrangement of the parts of a cell obeys a predetermined blueprint or design, as it does in a machine. Second, the conformational flexibility of most cellular constituents and the functional promiscuity [i.e. flexibility] they exhibit shows that a cell's operation is not as tightly constrained by its structural configuration as it is in a machine. Third, whereas a machine performs its function by precisely following a predefined sequence of steps, a cell can arrive at a particular end in a variety of ways: it can recruit different kinds of molecules to the same function – or the same kind of molecule to different functions – depending on the conditions it finds itself in. And fourth, a cell cannot be broken down into parts without jeopardizing its structural integrity in the way that every machine can. Cellular components form deeply intertwined, ever-changing networks of interactions that cannot be individually dissected without sacrificing the organization of the whole. (Nicholson, 2019, p. 123)

In other words, the cell's operation is emergent (Nizami, 2017, 2018). Indeed, the cell is what Heinz von Foerster calls a *non-trivial machine* (von Foerster, 1984, 2003). In place of *cell*, we could equivalently say *neuron* or *linked group of neurons.*

7.6 The Computer Metaphor: Non-Trivial Machines as Trivial Machines (Again)

Nicholson (2019) has detailed the pursuit of yet another inappropriate metaphor in which a trivial machine was used as a model for a non-trivial machine. That is, Nicholson (2019) examines

> the idea of the computer, which, by introducing the conceptual distinction between 'software' and 'hardware', directed the attention of researchers to the nature and coding of the genetic instructions (the software) and to the mechanisms by which these are implemented by the cell's macromolecular components (the hardware). (Nicholson, p. 109)

The computer can be classified, for argument's sake, as a trivial machine. The computer metaphor also lies at the heart of neuroscience—not per se because software directs hardware, but because of what software directs hardware to do within electronic circuits, namely, the steps called computation. Many researchers have actually imagined the mind itself to be a computer (reviewed in Nizami, 2018). Kline (2015) devotes pp. 44–49 of his history of cybernetics to describing some of the early post-1948 turbulence surrounding the arguments over whether computation in the nervous system was analog or digital, and indeed whether the metaphor of computation was valid at all.

The trivial-machine metaphor has lasted for decades. Why? As Nicholson explains,

> The methods traditionally used to probe the interior of the cell conceal the dynamic nature of its architecture because they have to incapacitate it in order to render it visible. Yet to study a cell frozen in time is already to approach it artificially as a static, machine-like object, rather than as the fluid system that it is in reality. (Nicholson, 2019, p. 112)

Or to approach it as a component of a rigid telecommunications system. Nicholson (2019, p. 112) continues, "The structure of a machine, after all, can be grasped in abstraction from time (as it is not constantly changing), whereas the structure of, say, a whirlpool or a stream cannot." As the whirlpool or the stream, consider the stochastic nature of the firing of voltage spikes by neurons in response to steady sensory stimuli. This is the neuron as a non-trivial machine.

8. Final words

8.1 The Bandwagon

Neuroscientists have abused information-theory terms, by simply re-labelling Shannon's system. Such relabelling also occurred and failed in psychology, as described by Keats (1966) and by Nizami (2009b, 2010a, 2011a, 2011b, 2012, 2013), and also in linguistics, as explained by Cretu (2008), amongst others. Relabelling has never justified the ultra-engineering calculations of information transmitted. Nor, as Nizami (2014b) points out, has any attempt at justification besides relabelling ever been offered. Shannon information theory is all about the general communication system, not about the meaning of whatever message is transmitted using it. Regardless, when Shannon information theory is used as Shannon had intended, all of its aspects have their own clear meanings, namely, those meanings assumed by communications engineers. When not used in this fashion, those meanings disappear. Indeed, in the everyday, street notion of the word *information*, the respective communication system is not what matters (in contrast to whatever mechanism produces the information's context, such as human behavior). Rather, what matters is a message's meaning.

Non-engineering manipulations of Shannon information theory arrived with remarkable haste (Dahling, 1962). This is reflected in the dates of the early entries in Table 1. Shannon (1956) was prompted to caution against adopting ultra-engineering extensions of information theory. This is highly ironic, given Weaver's introduction to

Shannon and Weaver (1949). In view of Shannon's near-immediate fame post-1948 (as documented in Kline, 2015), it is difficult to believe that Shannon had no say in what appeared in the first chapter of a book of which he was the lead author. Regardless, Weaver's and others' extensions of information theory beyond engineering were stretched yet-further by the popularization of an integral-calculus method for calculating information transmitted for neurons, a method explored and promoted in numerous papers authored by Rieke, Warland, de Ruyter van Steveninck, Bialek, and their various co-authors, culminating in the book *Spikes: Exploring the Neural Code* (Rieke et al., 1997). Such information-transmitted algorithms have become available in various software suites (see for example Goldberg et al., 2009; Ince et al., 2010; Effenberger, 2013; Cessac et al., 2017). Likewise, software for computation of Tononi's IIT is now freely available (Mayner et al., 2018). All of this allows neuroscientists having little or no training in math or physics to perform computation without comprehension (Nizami, 2016). That is, numbers can be produced with little attention to the underlying principles. Consider that neuroscience papers, if published after 1991, tend to cite just one source of the information theory math, out of more than twenty available textbooks: namely, Cover and Thomas (1991). Remarkably, Cover and Thomas never mention any use for information theory in the life sciences; likewise, it is exceedingly rare (with the exception of Nirenberg et al., 2001) that neuroscientists citing Cover and Thomas (1991) mention any specific page number, equation, passage, or concept, as if they had never read the book (Nizami, 2016). The present readers might likewise wonder whether the various authors citing *Spikes* had understood that tome, either (Nizami, 2016). The authors of *Spikes* were primarily physicists by training, not neuroscientists or biologists. But neuroscience, like law or medicine, is not something practised as a hobby.

8.2 Information as Failed Metaphor, and Its Consequences

The neuroscience establishment has a longstanding explanation for their use of Shannon information theory: "By analogy!" (Dahling, 1962). As Kline (2015, p. 152) explained it, "The central analogy of cybernetics [is the notion] that both humans and machines could be studied using the same principles from control and communications engineering." However, analogy is hope, not proof. In the case of information, the analogy altogether fails. The situation is synopsized in an insight from Wong (2007) regarding one particular information theory model of sensory neuronal firing, namely, the entropy theory of perception (Norwich, 1993). Wong (2007, p. 2) states that "little justification (beyond the simple analogy of the senses as a communications system) was provided for why information underlies the process of perception and why this result is universal." An earlier, broader view came from Rosen:

> It is well known that "information" is one of the murkiest and most overworked words in the scientific lexicon (perhaps only the word "model" can be compared to it). Indeed, there is almost no relation between the "information" of the Information Theory of Shannon (which beguiles many through its superficial relation to [thermodynamic] entropy), the "genetic information" upon which

> development, physiology and evolution devolve in their several ways, and the "information" appearing diversely in the functioning of the brain. (Rosen, 1985, p. 34)

Rosen's conclusions are just as fresh today.

Finally, we might ask what impact these informational misadventures have had on society at large. In this regard, Sullivan-Clarke (2019, p. 160) notes that "The issue of how to prevent scientists and their communities from being misled by metaphor and analogy has not only an epistemic component, but it takes on a moral one as well." The question of morality is well-exemplified in a paper that was not mentioned by Sullivan-Clarke, namely, Mudrik and Maoz (2014). Mudrik and Maoz explain another pervasive and misleading neuroscience metaphor, that of the brain and the self as having different mental states. The metaphor, in which the brain is anthropomorphized (Nizami, 2017), becomes a convenient excuse for deadly criminal acts ("my brain made me do it"). Of course, less-dangerous outcomes have arisen from metaphors, but such outcomes are disturbing, nonetheless. Consider the misuse of information in neuroscience, namely, the pursuit of the weak metaphors that any sensory stimulus is a symbol and that any interaction with symbols is communication. Consider particularly the long-term cost in money, time, and unfounded personal advancement. Here are some plausible numbers from the present author's experience. The number of peer-reviewed papers expounding information theory analyses of neuronal firing probably well-exceeds 1,000. A typical contemporary cost for such a study might be $30,000 United States dollars, most of it committed to salary. Altogether, that's $30,000,000 in total costs, as a minimum cost estimate—enough, at current salaries, to support 600 postdoctoral research fellows for an entire year. Then, there is the wasted time: hundreds of thousands of hours, spent primarily by the graduate students and postdoctoral research fellows who are responsible for running the relevant experiments, programming the calculations, and preparing the manuscripts and the associated conference presentations. And now we reach the most important factor: the number of people receiving academic promotions, some to tenured professorships, based on papers that present misleading information-theory analyses, all in a time of grotesque job shortages.

Note well that wasted money, wasted time, and undue promotion also characterize outright research fraud (Chevassus-au-Louis, 2019). Indeed, the cost of inappropriate metaphors can be extreme, insofar as metaphor-driven research may be used for social purposes that advantage some citizens while disadvantaging others; readers are left to peruse the examples that Sullivan-Clarke (2019) provides.

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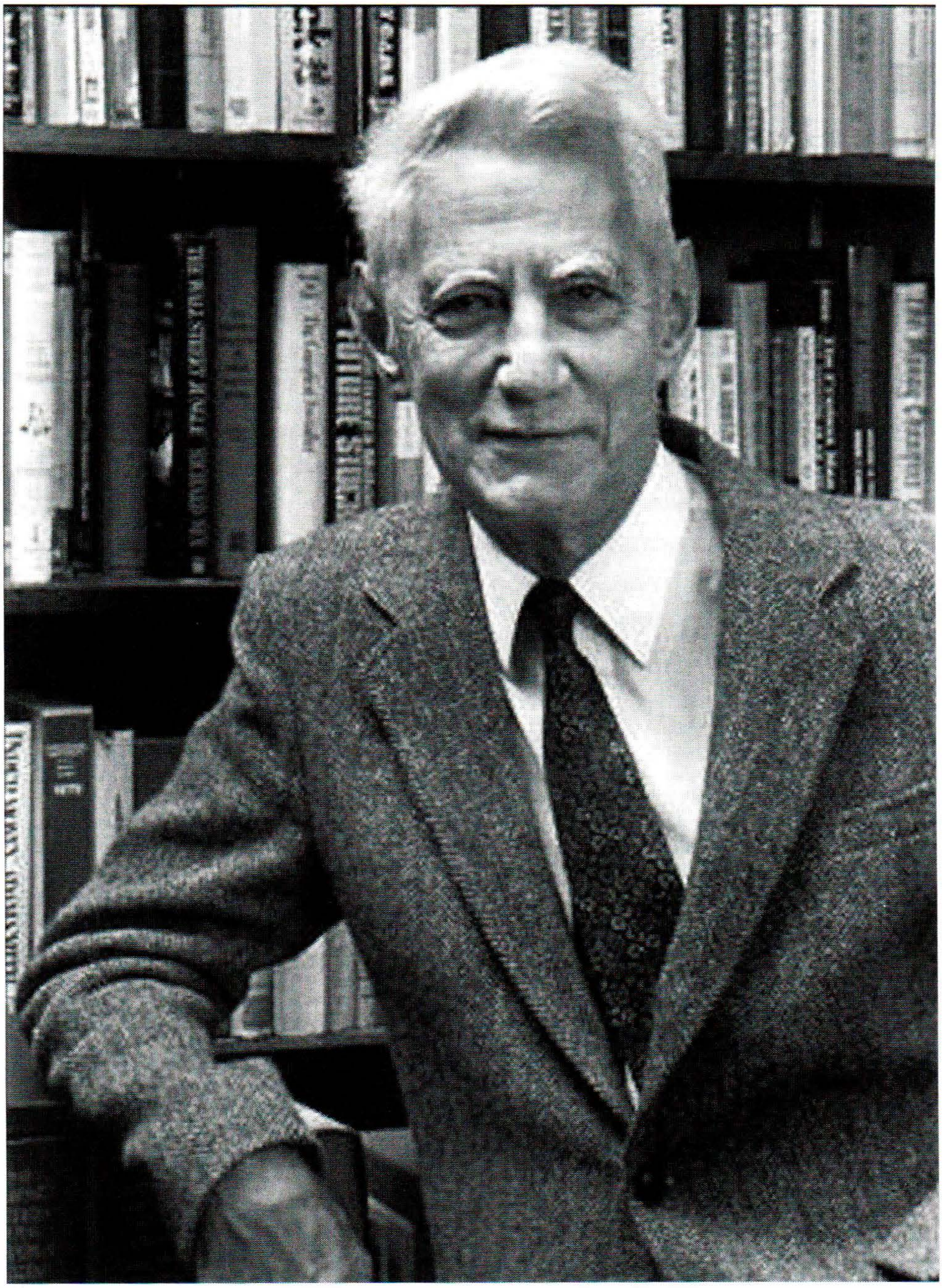


Claude Shannon (1916–2001)

Appendix: Table 1

Table 1: Neuroscientists' Interpretations of Elements of Shannon's General Communication System

Reference	Source	Transmitter	Channel	Noise Source	Receiver
1. Shannon & Weaver, 1949	Person (pp. 7, 10), "My brain" (p. 7)	Telephone/telegraph/ radio transmitter (p. 7), "A channel" (p. 18), "The voice mechanism", "Vocal system" (both p. 18)	Wire, space (both p. 7), The air (p. 7)	"Distortions of sound", "Static", "Errors in transmission" (all p. 8)	"Ear and the associated eighth nerve" (p. 7)
2. MacKay & McCulloch, 1952		"The nervous system" (p. 127), "Sensory fibers" (p. 133)	Synapse (p. 128)		
3. Rapoport, 1956			"A human being" (p. 310)		
4. Trucco, 1956		"Human subjects" (p. 317)	"Human subjects" (p. 317), "A human channel" (p. 319)		"Human subjects" (p. 317)
5. FitzHugh, 1957		"Communication channels" (p. 933), The source of a visual flash stimulus (p. 941)	"A ganglion cell, the photoreceptors of its receptive field, and the intermediate bipolar cells [all at the retina]" (p. 932)	"[In the eye] The unpredictable motion of the individual elementary particles of physics (atoms, ions, electrons, photons) ... [resulting from] thermal agitation or from events to which Heisenberg's principle of indeterminacy applies" (p. 925)	

Reference	Source	Transmitter	Channel	Noise Source	Receiver
6. Viernstein & Grossman, 1961		"Neurons" (p. 252)			
7. Kelly, 1962		"The human observer" (p. 221)	The retina, from "input radiation" to spike train "detector", "A living organism" (both p. 222)		"The human visual sense" (p. 221)
8. Hagins, 1965	Outer segment of photoreceptor cell (p. 403)		Body of photoreceptor cell (p. 403)	"Dark noise [the cell's internal noise]" (p. 405)	Synapse of photoreceptor cell with afferent neuron (p. 403)
9. Werner & Mountcastle, 1965		"Afferent fibers" (pp. 364, 392, 393)	"The skin" (p. 395)		
10. Stein, 1967		"Nerve cell or group of nerve cells" (p. 797), "Neuron" (p. 800)	"Nerve cell" (p. 799), "Neuron" (p. 800)	"Random fluctuations in the part of the neuronal cycle at which the stimulus begins ... [and] the duration of successive interspike intervals ... [and] the 'state' of the neuron" (p. 800; original internal quotation marks)	
11. Darian-Smith, Rowe, & Sessle, 1968		"Single trigemino-thalamic neurons" (p. 791)			

Reference	Source	Transmitter	Channel	Noise Source	Receiver
12. Durlach & Braida, 1969				"*Sensation noise* and *memory noise*. The sensation noise includes all the random elements in the transformation from the stimuli to the decision variable, except for those related to memory" (p. 374; original italics)	
13. Walløe, 1970		"Nerve cells" (p. 745), "The muscle" (p. 757), "Each primary afferent fiber" (p. 762)	"Chains of nerve cells" (p. 745), "The DSCT [dorsal spinocerebellar tract] neurons" (p. 746)		"The decoder" (pp. 747, 752), "One DSCT neuron" (p. 757), "A number of DSCT cells" (p. 762)
14. Walter & Gardiner, 1970		"Some sensory input" (p. 353), "The input S.V. [stochastic variable]" (p. 354), "Task" (p. 369)		"Irrelevant waves" (p. 357)	"A particular behavioral output" (p. 353), "The output S.V. [stochastic variable]" (p. 354), "Its correlates in the evoked response" (p. 369)
15. Harris & Stark, 1971			"A 1-cm photoreceptive nerve fiber" (p. 67)	"Ionic or anatomical noise in the nerve-membrane resistance or geometry" (p. 67)	
16. Kenton & Kruger, 1971		"An afferent channel" (p. 114)	"Nerve fibers" (p. 116), "The fiber" (p. 125)		

Reference	Source	Transmitter	Channel	Noise Source	Receiver
17. Eckhorn & Pöpel, 1974	"The stimulus at the input (eye) and the impulse train at the output, i.e. on the axon of the nerve cell" (p. 194)	"The signals" (pp. 191, 192), "Each single symbol" (p. 196), "Each actual pair of symbol sequences" (p. 196), "Consecutively emitted and received symbols" (p. 196)	"The visual system from the cornea to the recording site" (p. 194), "The eye including ganglion cells or the eye including the ganglion cell level and the LGN [lateral geniculate nucleus]" (p. 197)		
18. Eckhorn & Pöpel, 1975		"Ganglion cells and geniculate *P*-cells" (p. 7; also p. 15), "The investigated neuronal channel" (p. 8), "The on-center neuron … [or] the off-center neuron" (p. 11), "One impulse" (p. 11), "One stimulus" (p. 11), "The center stimulus" (p. 12), "Large area stimulation" (p. 12), "The discharge pause, and the following spontaneous discharge" (p. 13), "A presynaptic ganglion cell" (p. 13), "The system" (p. 14)	"The cornea to the recording site of the microelectrode, the dorsal lateral geniculate nucleus" (p. 7), "The axons" (p. 7), "A ganglion cell's axon" (p. 8)		

Reference	Source	Transmitter	Channel	Noise Source	Receiver
19. Lass & Abeles, 1975			“The [neuron’s] axon” (p. 61)	“Three sources of noise may be considered. First, the latent period between application of the stimulus and initiation of the action potential may be subjected to random variations … [Secondly] random variations in the velocity of propagation of the action potential along the axon …[Thirdly] the instrumentation used … [namely] internal noise of the peak detector” (p. 67)	“The *observer*” (p. 61; original italics)
20. Majernik & Kaluzny, 1975	“The set of external stimuli $S \equiv [s_1, s_2, \ldots, s_n]$ (acoustical signals) with its probability distribution $P \equiv [p_1, p_2, \ldots, p_n]$” (p. 175)				“The sensory space Z in which to each point a perception is coordinated” (p. 175)
21. Hannam & Farnsworth, 1977		“The periodontal innervation [the first order periodontal neurons]” (p. 181)			

Reference	Source	Transmitter	Channel	Noise Source	Receiver
22. Smith, Bowdan, & Dethier, 1983		"A chemoreceptor" (pp. 81, 82, 96), "[Neuronal voltage] Impulses" (p. 83), "The [insect's prothoracic] leg" (p. 94)			
23. Fuller & Looft, 1984		"A neuron" (p. 379)			
24. Eckhorn & Querfurth, 1985				"Fluctuation phenomena at the transducing and encoding sites" (p. 166)	
25. Optican & Richmond, 1987		"The spike count" (p. 162), "The neuron" (p. 163), "Different (uncorrelated) principal components [of the spike train]" (p. 163), "The response about a stimulus [*sic*] … the spike count code" (p. 168)	"The neuron" (pp. 163, 164)		
26. Georgopoulos & Massey, 1988		"The neuronal populations" (p. 317), "Movement direction" (of a target stimulus; p. 318)			

Reference	Source	Transmitter	Channel	Noise Source	Receiver
27. Bialek, Rieke, de Ruyter van Steveninck, & Warland, 1991				"Timing errors, dropped spikes, and spontaneously generated spikes" (p. 1856)	
28. Geisler, Albrecht, Salvi, & Saunders, 1991		Sensory neuron (p. 335)			
29. Theunissen & Miller, 1991	"A 'transmitter'" (p. 1691), "The air-current stimulus generator" (p. 1692)	"The air-current stimulus generator" (p. 1692)	"An ensemble of four neurons" (p. 1690)		A layer of neurons (p. 1692)
30. Skaggs, McNaughton, Gothard, & Markus, 1992			"A neuron" (p. 1036)		
31. Golomb, Kleinfeld, Reid, Shapley, & Shraiman, 1994			"The different temporal modes, or principle components [of the spike train]" (p. 2998)		
32. Heller, Hertz, Kjaer, & Richmond, 1995		"A neuron" (pp. 175, 176, 188)	"The neuron" (p. 175)		"Other neurons" (p. 175)
33. Rieke, Bodnar, & Bialek, 1995		"Primary sensory afferent spike trains" (p. 259), "Sensory neurons" (p. 263)			
34. Roddey & Jacobs, 1996		"The interneurons" (p. 1376)			

Reference	Source	Transmitter	Channel	Noise Source	Receiver
35. Waters, 1996				"The spontaneous generation of action potentials within its [a moth's] own auditory system" (p. 864)	
36. De Ruyter van Steveninck, Lewen, Strong, Koberle, & Bialek, 1997		The neuron (p. 1807)			
37. Juusola & French, 1997		"Sensory systems" (p. 959)			
38. Rieke, Warland, de Ruyter van Steveninck, & Bialek, 1997	"The outside world" (p. 104)	"Sensory neurons" (p. 101), "The spike train" (p. 101), "The system" (p. 148), "Vesicles at a chemical synapse" (p. 187), "[number of] Spikes" (p. 187)	"The device we are trying to characterize" (p. 102)		"We" (p. 104)
39. Warland, Reinagel, & Meister, 1997		"Retinal ganglion cells" (p. 2336), "Spike train" (pp. 2343, 2346), "The summed signal [of a cone photoreceptor]" (p. 2348)		"The output of the cone photoreceptor" (p. 2348)	"The brain" (p. 2336)
40. Strong, Koberle, de Ruyter van Steveninck, & Bialek, 1998		Spike train (pp. 197, 199)			
41. Wiener & Richmond, 1998		"A channel" (p. 281)	"The neuronal responses" (p. 281)		

Reference	Source	Transmitter	Channel	Noise Source	Receiver
42. Zador, 1998		"A retina" (p. 1228)		"The probability [symbol omitted] that a glutamate-filled vesicle is released after presynaptic activation may be less than unity ... [and also] the post-synaptic current in response to a vesicle may vary even at single individual terminals" (p. 1220)	
43. Reinagel, Godwin, Sherman, & Koch, 1999		"An LGN [Lateral Geniculate Nucleus] response [spike train]" (p. 2561), "Thalamocortical synapses" (p. 2568)			
44. Baddeley, 2000	"The time-varying membrane potential" (p. 5)	"A representation" (p. 14), "An insect eye" (p. 14)		"The random nature of photon arrival or the unreliability of synapses" (p. 16)	
45. Burton, 2000		"The early visual system" (p. 26), "A single neuron" (p. 26), "The channel" (p. 26), "The ganglion cell" (p. 33)	"The optic nerve" (p. 25), "Ganglion cells" (p. 38)	"The standard deviation in photon count" (p. 26), "Synaptic transmission" (p. 27)	

Reference	Source	Transmitter	Channel	Noise Source	Receiver
46. Eguia, Rabinovich, & Abarbanel, 2000		"Environment" (p. 7111)	"Neural communications channels" (p. 7111), "One neuron" (p. 7112), "A neuron that receives the spike train, a synaptic connection, and a receiver that is another neuron" (p. 7113), Synapse (p. 7114)		"Decision centers" (p. 7111), "The receiver neuron" (p. 7112), Any neuron (p. 7114)
47. Laughlin, Anderson, O'Carroll, & de Ruyter van Steveninck, 2000		"A blowfly photoreceptor or a retinal interneuron" (p. 41), "A neuron" (p. 42), "The graded responses of a single blowfly photoreceptor" (p. 46), "Second-order neurons called LMCs [large monopolar cells]" (p. 50), "Graded responses of LMCs" (p. 50), "Biological systems" (p. 54), "A single protein" (p. 54), "Action potentials" (p. 54)	"A small, low-information-capacity synapse" (p. 52), Axon of LMC (p. 53)		
48. Baird, Taube, & Peterson, 2001	The environment (p. 1031)	"[Neural] cells acting alone and together" (p. 1028)			
49. Rogers, Runyan, Vaidyanathan, & Schwaber, 2001		"The spike train" (pp. 450, 457)			

Reference	Source	Transmitter	Channel	Noise Source	Receiver
50. van Rullen & Thorpe, 2001		"Neurons" (p. 1255)	"The optic nerve" (p. 1261)		
51. Wiener, Oram, Liu, & Richmond, 2001		"The neuron" (p. 8212)			
52. Furukawa & Middlebrooks, 2002		"Three unidimensional parameters: mean spike count, mean spike latency, and the dispersion of spike latency" (p. 1750), "Each unit [i.e., relevant neuron]" (p. 1753)			
53. Averbeck, Crowe, Chafee, & Georgopoulos, 2003		"Single neurons and ensembles" (p. 143), "Single neurons and small neuronal ensembles" (p. 145), "A system with a given amount of noise" (p. 150)			
54. Chacron, Longtin, & Maler, 2003				"Channel and synaptic noise" (p. 821)	
55. Hsu, Woolley, Fremouw, & Theunissen, 2004		"The responses of single neurons" (p. 9202), The entropy of "the distribution of the magnitude of the time-varying mean firing rate" (p. 9206)		"Variability over trials of the neural response" (p. 9204)	

Reference	Source	Transmitter	Channel	Noise Source	Receiver
56. Lu & Wang, 2004		"Neurons" (p. 309)			
57. Osborne, Bialek, & Lisberger, 2004		"A cell" (p. 3212)			
58. Passaglia & Troy, 2004		"Retinal ganglion cells" (p. 1219)	"A spiking neuron anywhere in the nervous system" (p. 1228)		"Target neurons in the brain" (p. 1217)
59. Nelken, Chechik, Mrsic-Flogel, King, & Schnupp, 2005		"Neurons in auditory cortex" (p. 199), "Spike count" (p. 216)			
60. Arabzadeh, Panzeri, & Diamond, 2006		"Neurons" (pp. 9216, 9217)			
61. Koch, McLean, Segev, Freed, Berry II, Balasubramanian, et al. 2006		"Brisk-transient ganglion cells" (p. 1431)	"Individual ganglion cells" (p. 1431)		
62. Victor, 2006		Neurons (p. 303)	Neurons (p. 304)		
63. Sadeghi, Chacron, Taylor, & Cullen, 2007		Afferents (pp. 771, 774, 777)			

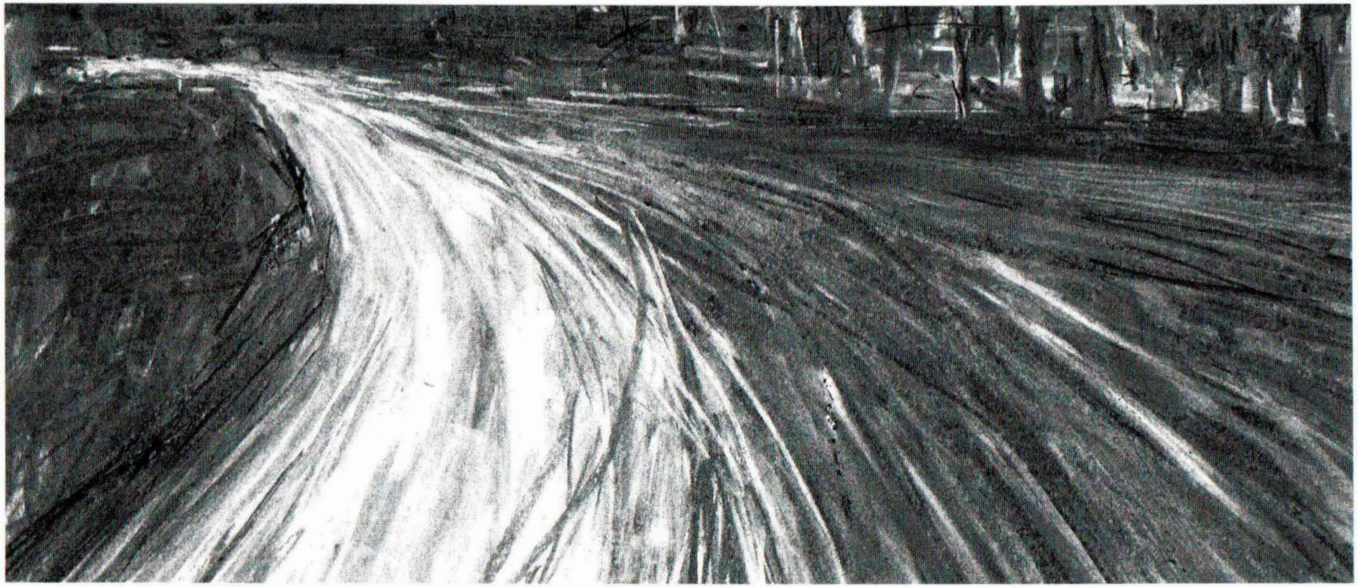
Reference	Source	Transmitter	Channel	Noise Source	Receiver
64. Eyherabide, Rokem, Herz, & Samengo, 2008		"Each event" (p. 5), "Each single *n*-burst" (pp. 5, 16) where the latter is "The set of consecutive spikes whose ISIs [inter-spike intervals] fell within the domain of the first peak of the correlation function" (p. 4), "Burst firing" (pp. 11, 13), "A code based on the intra-burst spike count *n*" (p. 15)			
65. Johnson, 2008	"Stimulus/motion generator" (p. 104)	"Encoder" (p. 104)	"A neuron or a population of neurons" (p. 104); "a jointly defined multi-dimensional point process" (p. 104)	"Stimulus/motion decoder" (p. 104)	
66. Ikeda & Manton, 2009			"A single neuron" (p. 1714)		
67. Saal, Vijayakumar, & Johansson, 2009		"Spike counts and spike timing" (p. 8022), "Afferents" (p. 8026), "The timing of only the first spikes elicited in tactile afferents" (p. 8028), "Firing rates" (p. 8028), "Precise spike timing and firing rates" (p. 8029)	"Individual afferents" (p. 8023)		

Reference	Source	Transmitter	Channel	Noise Source	Receiver
68. McDonnell, Burkitt, Grayden, Meffin, & Grant, 2010	"The place of stimulation" on an electrode array implanted in the inner ear (p. 932)		"The interface between an electrode array and the auditory nerve" (p. 928), "Each individual fiber" in the auditory nerve (p. 930), "1) A mechanism for conversion of place of stimulation into electrical activity in the auditory nerve; 2) processing of auditory nerve activity that is carried out by higher levels of the brain, including the auditory brainstem and auditory cortex" (p. 932)		
69. Lawhern, Nikonov, Wu, & Contreras, 2011		"The periphery [the peripheral sensory organs – eyes, nose, etc.]" (p. 1)			
70. McDonnell, Ikeda, & Manton, 2011	"Spoken voice or PDF (portable document format) documents" (p. 4). "The 'input'" (p. 10)	"The brain" (p. 3), "Cortical neurons" (p. 10), "spikes" (p. 15)	"A neuron" (p. 9)	Randomness of the inter-spike time interval (p. 11), "internal noise in the transduction mechanisms" (p. 12)	"Cortical neurons" (p. 10), neurons (p. 14)

Reference	Source	Transmitter	Channel	Noise Source	Receiver
71. Aldworth, Bender, & Miller, 2012		"Neuron" (p. 6)	"The axon [of the neuron] itself" (p. 1), "Short ISIs [inter-spike-intervals]" (p. 8), "Nervous systems" (p. 8)	"Temporal uncertainty arising from AP [action potential] conduction (transmission jitter), AP acceleration due to a supernormal period, AP deceleration due to refractory effects, and AP conduction failures" (p. 1; see also p. 2)	
72. So, Ganguly, Jimenez, Gastpar, & Carmena, 2012		"A redundant encoding scheme at the [neural] ensemble level" (p. 556)			
73. Effenberger, 2013		"Neurons" (p. 138), "A communication channel" (p. 157), "The source" (p. 167)	"Neurons" (p. 178), "Synapses" (p. 178), "The early sensory pathway" (p. 182)		
74. Faghihi, Kolodziejski, Fiala, Wörgötter, & Tetzlaff, 2013		"The antennal lobe [of *Drosophila* fruit flies]" (p. 1), "The *Drosophila* olfactory system" (pp. 2, 3)	"The antenna and antennal lobe" (p. 2), "The *Drosophila melongaster* [*sic*] olfactory system" (p. 3)		
75. Farfán, Albarracín, & Felice, 2013				"The recording hardware, the recording environment and the spatially averaged activity of distant axons" (p. 95)	

Reference	Source	Transmitter	Channel	Noise Source	Receiver
76. Garcia-Lazaro, Belliveau, & Lesica, 2013		"The cells" (p. 19366)			
77. Aldworth & Stopfer, 2015		Projection neurons (pp. 1521, 1527), "The system" (p. 1521)			
78. Jadzinsky & Baccus, 2015		"Ganglion cells" (p. 1), "The neural code" (p. 2)			
79. Kostal & Kobayashi, 2015		The neuron (p. 3)	"The neuron" (p. 3)		
80. Wibral, Lizier, & Priesemann, 2015		"Specific neural responses" (p. 5)			
81. Rathkopf, 2017	"An environmental property" (p. 322)	"A single perceptual neuron" (p. 322); "strings … for example, a long binary string [of ones and zeros]" (p. 331)			"A motor neuron … which controls locomotion" (p. 322)
82. Wang, Borst, Zaslavsky, Tishby, & Segev, 2017		"The H1 neuron" (p. 13), "The photoreceptors" (p. 16)			

Reference	Source	Transmitter	Channel	Noise Source	Receiver
83. Liu, Yue, Yu, Liu, & Yu, 2018		"The neurons" (pp. 220, 223–225), "APs [action potentials]" (p. 229)		"The inner noise source is mainly from the stochastic gating of the ion channels" (p. 219)	
84. Voronenko & Lindner, 2018		"Neurons" (p. 1)			



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