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I, NEURON: the neuron *as* the collective

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Abstract

Purpose – In the last half-century, individual sensory neurons have been bestowed with characteristics of the whole human being, such as behavior and its oft-presumed precursor, consciousness. This anthropomorphization is pervasive in the literature. It is also absurd, given what we know about neurons, and it needs to be abolished. This study aims to first understand how it happened, and hence why it persists.

Design/methodology/approach – The peer-reviewed sensory-neurophysiology literature extends to hundreds (perhaps thousands) of papers. Here, more than 90 mainstream papers were scrutinized.

Findings – Anthropomorphization arose because single neurons were cast as "observers" who "identify", "categorize", "recognize", "distinguish" or "discriminate" the stimuli, using math-based algorithms that reduce ("decode") the stimulus-evoked spike trains to the particular stimuli inferred to elicit them. Without "decoding", there is supposedly no perception. However, "decoding" is both unnecessary and unconfirmed. The neuronal "observer" in fact consists of the laboratory staff and the greater society that supports them. In anthropomorphization, the neuron becomes the collective.

Research limitations/implications – Anthropomorphization underlies the widespread application to neurons Information Theory and Signal Detection Theory, making both approaches incorrect.

Practical implications – A great deal of time, money and effort has been wasted on anthropomorphic Reductionist approaches to understanding perception and consciousness. Those resources should be diverted into more-fruitful approaches.

Originality/value – A long-overdue scrutiny of sensory-neuroscience literature reveals that anthropomorphization, a form of Reductionism that involves the presumption of single-neuron consciousness, has run amok in neuroscience. Consciousness is more likely to be an emergent property of the brain.

Keywords Consciousness, Anthropomorphization, Observer, Decoding, Neuron, Reductionism

Paper type Research paper

1. Introduction

The anthropomorphization of the neuron is defined as the casting of the neuron as a human being. As such, the neuron hypothetically does things that are done by awake, alert and behaving human beings. Here, "behaving" implies conscious choices, not mere reflexes.

The anthropomorphization of *parts* of the human body undoubtedly began in ancient times. However, the modern anthropomorphization of some or all of the *sensory nervous system* has an identifiable origin, namely, "What the frog's eye tells the frog's brain" (Lettvin *et al.*, 1959). In this alleged *conversation*, a behavioral output (speech), which might be encouraged by sensations (here, the percepts that are images), in fact replaces the voltage spikes that triggered those selfsame images. This rearrangement of cause-and-effect is laughable. And yet it is taken seriously and is pervasive; among the 2,170+ citations of Lettvin *et al.* (1959) (GoogleScholar) – well-above the 100-count that already represents above-average popularity in the field – consider "What the frog's eye tells the human brain"

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(Weisstein, 1969), "What the frog's eye tells the monkey's brain" (Humphrey, 1970), "What the retinal ganglion cells tell the visual cortex" (van Rullen and Thorpe, 2001), "What the frog's nose tells the frog's brain" (Restrepo, 2004), "How *much* the eye tells the brain" (Koch *et al.*, 2006; original italics) and "What the [rodent's] whiskers tell the tactile brain" (Estebanez *et al.*, 2014).

Such titles perpetuate the liberties taken by Lettvin *et al.* (1959). Anthropomorphization is a form of metaphor, i.e. a literary device. Anthropomorphization also represents a lack of scientific distinction. At first, this might be blamed upon laziness. But anthropomorphization is a form of Reductionism (more on this below), and it connotes shades of religious belief, in particular the puerile, unsupported notion that individual neurons are *conscious* (animism). Hence anthropomorphization distracts from other, more credible explanations for consciousness and the mind, as will be shown.

How can we successfully abandon anthropomorphization? To do so, we must first understand why it persists, which in turn requires understanding how it entered the literature in the first place. To those ends, the present work scrutinizes more than 90 central peer-reviewed sensory-neuroscience articles, many of them highly cited, taken from respected sources in a literature which extends to thousands of documents. Sometimes quotations are used to capture the original flavor of the work, as well as to avoid any accusation of misrepresentation. The "present tense" is used, also, because the subject matter remains fresh. Some unexpected insights arise from this critical examination.

2. The decision-making, criterion-holding neuron

The investigation formally begins not with Lettvin *et al.* (1959), but nonetheless in the same year, with Professor Theodore H. Bullock's influential contribution to the seminal 1959 *MIT Symposium on Principles of Sensory Communication* (published in 1961, as *Sensory Communication*; re-printed in 2012; countless citations). Bullock (1961, p. 718) imagines a population of higher-level neurons – that is, neurons perhaps closer to the brain than to the eye, ear, nose, tongue or skin – in which each neuron is a "decision" unit. That is, each neuron is "like a military general" (Bullock, 1961, p. 718), insofar as it must "deliver an unequivocal answer" about whether some "criterion" is met for further neuronal action (Bullock, 1961, p. 718) (an action, for example, such as activating a physical movement). To Bullock (1961, p. 719), "Every neuron is a *decision-making element* when it changes from a silent to an impulse–firing state" (Bullock, 1961, p. 721; italics supplied). Again, according to Bullock, this represents "recognition of a predetermined criterion" (Bullock, 1961, p. 724).

Figure 1 represents a typical sensory-neurophysiology experiment. Stimuli are applied to a test animal by the neuroscientist/experimenter. The animal's receptors (e.g. cone photoreceptor cells in the eye or inner-hair-cells in the ear) each synapse with (i.e. electrically connect to) one or more parallel "primary afferent" neurons, which produce a train of voltage spikes which follow along subsequent afferent (i.e. brain-going) neurons, in a chain leading to the brain. Any of those neurons may be "tapped" using an electrode to record the voltage-spike train for examination.

Remarkably, Bullock's (1961) "recognition of a predetermined criterion" *by single neurons* is still proselytized (Barlow, 1994). The notion even infiltrates books that promote "systems views" of biology (for example, Miller, 2015, p. 115). Indeed, Bullock's notion appears often in the sensory-physiology literature, reworded as "discriminating" and/or "distinguishing" (Werner and Mountcastle, 1965 [490+ citations], p. 382; Darian-Smith *et al.*, 1968; Walløe, 1970; Kenton and Kruger, 1971; Hannam and Farnsworth, 1977; Golomb *et al.*, 1994; Heller *et al.*, 1995 [190+ citations], p. 192; Gnadt and Breznen, 1996; Buračas *et al.*, 1998 [370+ citations]; Gehr *et al.*, 2000; Averbeck *et al.*, 2003; Chacron *et al.*, 2003, p. 804; Osborne *et al.*,

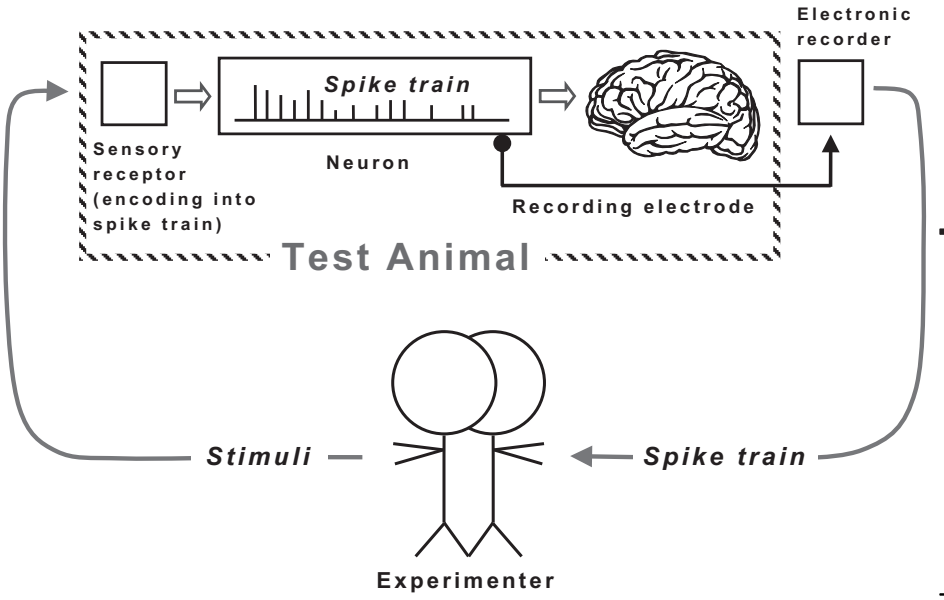

Figure 1. Schematizes the kind of experiments that Lettvin *et al.* (1959) and Bullock (1961) and their successors performed

2004 [120+ citations]; Faghihi *et al.*, 2013, p. 5). For example, a neuron "distinguishes the current stimulus from other candidates" (Arabzadeh *et al.*, 2004 [130+ citations], p. 6011); more specifically, "Single auditory neurons rapidly discriminate conspecific communication signals" (Machens *et al.*, 2003, p. 341).

3. The detective, informant, journalist, grandmother, messenger, marketer or signalman

The anthropomorphization of the neuron has many forms. The neuron "recognizes" (Werner and Mountcastle, 1965, p. 383). The neuron "detects", as if a detective (Crick and Koch, 2003 [1,270+ citations], p. 120; Sadeghi *et al.*, 2007, p. 779) or (in a similar vein) is said to "identify" (Darian-Smith *et al.*, 1968; Kenton and Kruger, 1971; Gochin *et al.*, 1994 [160+ citations], p. 2327; Rolls *et al.*, 1996 [120+ citations]; conveys "levels of information about stimulus identity" in Chechik *et al.*, 2006 [170+ citations], p. 361). To Saal *et al.* (2009, p. 8029), the neuron is "highly informative", as if an informant. The neuron "reports", as if a journalist (Arabzadeh *et al.*, 2004, p. 6011; for the whole retina in Warland *et al.*, 1997 [380+ citations], p. 2336, after the style of Lettvin *et al.*, 1959). Neurons are said to "discover" (Gütig, 2016). Neurons can even be "grandmotherish" (Skaggs *et al.*, 1992 [320+ citations], p. 1031), after another notion from the Lettvin laboratory (Barlow, 1994), namely, the "grandmother neuron".

The notion from Lettvin *et al.* (1959) of *conversing neurons* permeates the literature. The neuron "tells" (Naka and Sakai, 1993, p. 75; Rieke *et al.*, 1997 [2,880+ citations], p. 102). It "communicates" (Passaglia and Troy, 2004, p. 1227; e.g. "to other neurons" in Rolls *et al.*, 2010, p. 23). That is, "Neurons must *communicate* voltage signals to one another through their connections (synapses)" (Burton, 2000/2008, p. 25; italics supplied); indeed, the eye's retinal ganglion cells are, after Lettvin *et al.* (1959), "communicating the incoming light pattern to the cortex and beyond" (Baddeley, 2000/2008, p. 5). Notwithstanding what might

be "beyond" the cortex (e.g. neuronal feedback loops?), an afferent sensory neuron generally "communicates information" (Atick and Redlich, 1990 [480+ citations], p. 311) or it "conveys information" (MacKay and McCulloch, 1952 [340+ citations]; Walløe, 1970, p. 746; Tolhurst, 1989, p. 409; Gochin *et al.*, 1994; Rieke *et al.*, 1997, p. 101; Arabzadeh *et al.*, 2006 [130+ citations], p. 9217; Victor, 2006; Saal *et al.*, 2009, p. 8022), or it "carries information" (McClurkin *et al.*, 1991 [140+ citations]; Heller *et al.*, 1995; Arabzadeh *et al.*, 2004, p. 6012; Rolls *et al.*, 2010, p. 23). But to emphasize the actual information carrier: "A *train of spike discharges* contains and communicates complex information to the brain" (Naka and Sakai, 1993, p. 78; italics supplied). The spike train ostensibly contains *messages* (Optican and Richmond, 1987 [390+ citations]; van Rullen and Thorpe, 2001 [410+ citations]). Of course, messages are a tool of propaganda, and neurons *manipulate* information (Victor, 2006, p. 313) – as if a marketer or a propagandist.

How exactly is "information" to be "communicated" if the distances are long? The answer is that the neuron "signals", as if a signalman on a train, aircraft or sailing-vessel (Werner and Mountcastle, 1965, p. 395; Kenton and Kruger, 1971; Hannam and Farnsworth, 1977; Naka and Sakai, 1993, p. 76; Averbeck *et al.*, 2003, p. 145; Passaglia and Troy, 2004, p. 1217; Aldworth *et al.*, 2012, p. 6; for cortical stages, see Tovée *et al.*, 1993 [300+ citations], p. 648).

Figure 2 shows the neuron in some of its many roles.

4. Interim summary: I, Neuron

Individual neurons have been cast as human beings. Neurons allegedly decide, judge, recognize, categorize, detect, distinguish and/or discriminate. Neurons are military generals, detectives, informants, journalists, grandmothers, messengers, marketers or signalmen.

Why did these attributions occur?

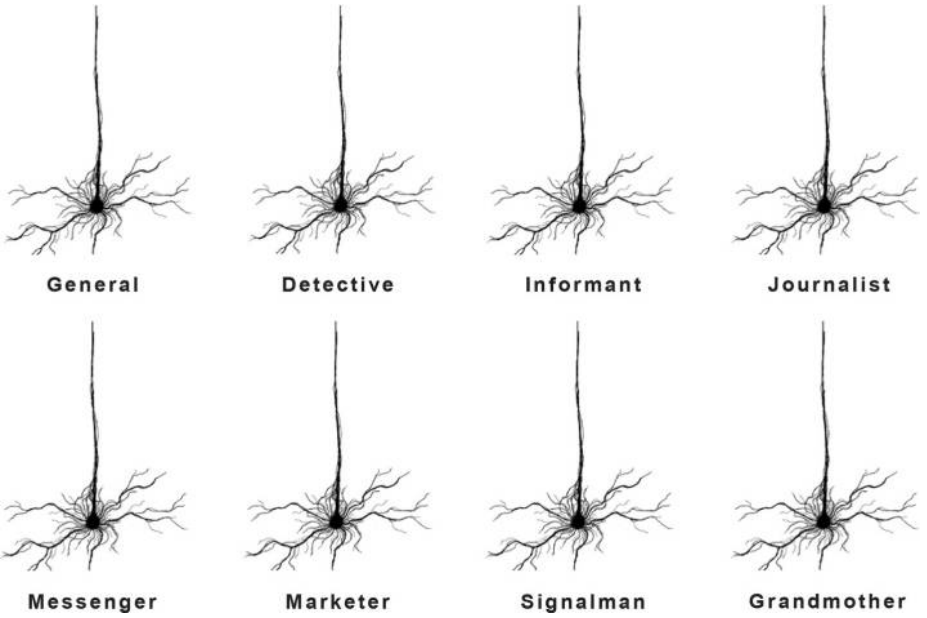

Figure 2.
The neuron (here, one more-typical of the brain), acting in its many roles

5. Understanding anthropomorphization: introducing the observer of the neuronal spike train

In understanding the reasons underlying the anthropomorphization of the neuron, the most convenient place to start is not at the historical beginning of neurophysiological recordings (roughly a century ago) but rather with MacKay and McCulloch (1952). MacKay and McCulloch explored a central tenet of neuroscience, namely, that if a single neuron's rate of firing of voltage spikes is sensitive to some measurable characteristic of the stimulus then that respective firing rate (or something derived from it) may reflect that respective stimulus characteristic. An example of "stimulus characteristic" is the intensity of a sinusoidal sound-pressure-wave (a pure tone), represented in the voltage-spike-firing *rates* of the most peripheral afferent auditory neurons (Nizami, 2002, 2003, 2005a, 2005b, 2014, 2015a, 2015b; Nizami and Schneider, 1997, 2000).

MacKay and McCulloch (1952, p. 132) seek to infer "the number of possibilities distinguishable by the receiver". The word "receiver" appears importantly elsewhere as "central detector" (Werner and Mountcastle, 1965, p. 388, p. 392). More importantly yet, the receiver/detector appears also as the *observer*. For example, Heller *et al.* (1995, p. 188) ask, "How much could be determined about the stimulus by *observing* the response for a specific amount of time?" (italics supplied), supposing that "The messages transmitted by single neurons need to be read" (Heller *et al.*, 1995, p. 188) so that stimulus features "can be discriminated on the basis of a neuron's response" (Heller *et al.*, 1995, p. 192). In Lass and Abeles (1975), the observer examines the spikes arriving at the (colloquially) "downstream" end of any single neuron of the frog's sciatic nerve, and "tries to deduce" (Lass and Abeles, p. 61) what "upstream" spike-evoking electrical impulses were applied (by the experimenters). Van Rullen and Thorpe (2001, p. 1257) echo Lass and Abeles (1975): "We take the position of an imaginary observer 'listening' to the pattern of spikes coming up the optic nerve and trying to derive information about the input image" (original internal quotation marks). Likewise, Arabzadeh *et al.* (2006, p. 9216) mention "an observer who 'reads off' the spike train signals" (original internal quotation marks).

Victor (2006), a math modeler, summarizes many ways in which "an observer of the neural response" (Victor, 2006, p. 304) allegedly "derives information". Unfortunately, Victor and other authors fail to mention who/what is the observer. Hence, the following analysis.

6. Understanding anthropomorphization: the observer "decoding"

6.1 "Decoding" or "reconstruction" or "estimation" of the stimulus

In an influential early paper, Stein (1967 [230+ citations], p. 824) declares that "information is *decoded*" (italics supplied). "Decoding" is also called "reconstruction". Regardless of name, it ostensibly takes "information" and makes it "available to higher order neurons" (Stein, 1967, p. 824). That is, reconstruction is *by neurons for neurons*. There is much to say about this. Arabzadeh *et al.* (2004, p. 6015), echoing Stein, assume that "Decoding must occur for the successful transmission of information from one group of neurons to a second group".

Reconstruction is no passing fad; Rogers *et al.* (2001, p. 448) declare that accurate reconstruction is "The central problem for the neurophysiologist". If so – given a chain of neurons, leading from a sensory receptor cell up into the brain – what is *ultimately* reconstructed, and why? MacLeod *et al.* (1998 [270+ citations], p. 693) explain (original internal quotation marks):

> Our inferences about brain mechanisms underlying perception rely on whether it is possible for the brain to "reconstruct" a stimulus from the information contained in the spike trains from many neurons.

So, it is the *stimulus* that is ultimately reconstructed! As Zhang *et al.* (1998 [440+ citations], p. 1017) declare (italics supplied):

> Reconstruction is a useful strategy for analyzing [the] data recorded from populations of neurons, in which external physical variables such as the orientation of a light bar on a screen, the direction of hand movement in space, or the position of a freely moving animal in space are *estimated* from brain activity.

So, at the brain, "decode" and "reconstruct" are effectively synonymous with "estimate". Or identify, or recognize, or categorize, or distinguish, or discriminate or whatever. But these are anthropomorphic capabilities, and further, they are often assigned to single, *often peripheral*, neurons, which would altogether leave the brain with nothing to do. This issue is important and will be revisited later. Meanwhile, the brain is kept busy by Seriès *et al.* (2009, p. 3273), who simplify decoding to a two-step process:

> We assume that perception can be described using an encoding-decoding cascade. The encoding stage represents the transformation between the external sensory stimuli and the activity of a population of neurons in sensory cortex, while the decoding stage represents the transformation from that activity to a perceptual estimate.

The meaning of "perceptual estimate" was left unexplained; the implication (there and elsewhere), however, is that perception *is* estimation. The idea of the senses as "estimators" recurs frequently in the literature (for many examples, see Baddeley, 2000/2008).

Figure 3 schematizes "reading" and "decoding" according to neuroscientists.

6.2 "Estimates" by observers: neuron(s) observing neurons

How is "estimation" done? Rieke *et al.* (1995 [270+ citations], p. 263) represent long-standing assumptions when they ask "how accurately an *observer* of the spike train in a single [sensory] afferent can estimate the sensory stimulus" (italics supplied). So, the estimator is the *observer*. But the *observer* is where, or whom, or what, in practicality? Bialek *et al.* (1991 [1,020+ citations], p. 1854) answer: "All of an organism's information about the sensory world comes from real-time observation of the activity of its own neurons". To repeat: *real-time observation of the activity of its own neurons*. Again, reconstruction is by neurons for neurons. But which neurons observe which? For flies, the motion-sensitive neurons of the eye – *or* the neurons that they connect to, brain-ward – can "read" a hypothetical "neural code" (Bialek *et al.*, 1991, p. 1855), making them observers (of neural codes).

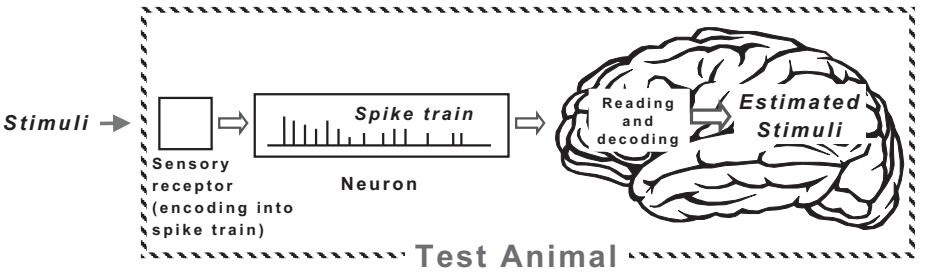

Figure 3.
"Reading" and "decoding" (see text and compare to Figure 1), which allows the animal to "estimate the stimulus". Such estimates are, of course, not the actual stimuli (which are flashes of light, sound-pressure waves, etc.)

Observation of neurons and decoding *by* neurons has been promoted well into the twenty-first century (DiCaprio *et al.*, 2007; Aldworth *et al.*, 2012; So *et al.*, 2012). Averbeck *et al.* (2003, p. 143) spoke of "how many levels of a behavioral factor [. . .] can be discriminated *by* the activity of single neurons or small ensembles [i.e. through decoding]" (italics supplied). Arabzadeh *et al.* (2004, p. 6015) echo Bialek *et al.* (1991) when they wonder "how the response of a barrel cortex neuronal population [i.e. in a rat's brain] could be most efficiently decoded, or 'read off', by the target neurons" (original internal quotation marks). The "target neurons" were not named – which is not surprising, given that barrel-cortex neurons are found at the cortex, hence being "target neurons" themselves. Passaglia and Troy (2004, p. 1217) echo Lettvin *et al.* (1959) when they declare that "Retinal ganglion cells [. . .] encode their messages with trains of optic nerve impulses [i.e. spike trains], which target neurons in the brain must *decipher* in a reliable and timely manner" (italics supplied).

7. Neuron as observer as neuroscientist

7.1 "Estimates" as guesses by observers

How is decoding done, in practicality? Bialek *et al.* (1991) tell us that neurons "read" a hypothetical "neural code" by means of "building a (generally nonlinear) filter that operates continuously on the spike train to produce a real-time estimate of the unknown stimulus waveform" (Bialek *et al.*, 1991, p. 1855). That is quite something, and of course it is what Bialek *et al.* (or their assistants) do in the laboratory to produce "perceptual estimates". Bialek *et al.* presume that *individual neurons, or the whole brain itself, do what scientists accomplish altogether as a laboratory collective, with the indispensable support of an entire society*. The Bialek *et al.* presumption is typical of the literature. For example, Walløe (1970, p. 747) states that "The decoder receives a train of impulses and makes estimates about the mean frequency [i.e. of spike firing in the neuron]", but on his next page Walløe reveals his mean-frequency equations, thereby revealing himself as the actual decoder. Osborne *et al.* (2004, p. 3210, p. 3218) speak of what neurons can discriminate, but they betray who does the discriminating when they mention "the average extent to which the neural response allows *us* to identify the stimulus" (p. 3212; italics supplied). Similarly, Seriès *et al.* (2009, p. 3275) refer to an "aware decoder", the word "aware" suggesting one or more of the Seriès *et al.* staff. The literature abounds in such examples.

Reconstruction algorithms, such as those used by Bialek *et al.* (1991), are based upon mathematical models. The models are varied, numerous and too complicated to describe here; Victor (2006) provides a long review, one which only partially covers the gamut. This plethora suggests some underlying uncertainty on the part of the authors – and indeed, "The intrinsic neuronal code that carries visual information and the perceptual mechanism for decoding that information are not known" (McClurkin *et al.*, 1991, p. 675). Nor are they known for any other senses. Hence, "perceptual estimates" are man-made *guesses*. This is rarely admitted and slyly so. For example, Alkasab *et al.* (1999, p. 103) express their desire to quantify "how much better than chance an observer could guess the stimulus" from neuronal spike trains. Likewise, Wiener *et al.* (2001, p. 8215) wonder "how well an observer can guess which stimulus elicited any particular observed [neuronal] response". Similarly, Nelken *et al.* (2005 [130+ citations], p. 200) use a putative decoder that "receives a spike train as input and guesses which stimulus evoked the spike train".

Recall from above "the perceptual mechanism for decoding" (McClurkin *et al.*, 1991, p. 675), namely, the observer who makes guesses – who is the *experimenter* (Nizami, 2014, 2015a). Consider that the "receiver" of MacKay and McCulloch (1952), for example, is actually one or both of MacKay or McCulloch – whomever observed and analyzed the recorded spike trains. In Lass and Abeles (1975), likewise, the "observer" is one or both of

Lass and Abeles. If this point remains unclear, consider a few simple word-substitution exercises. Chechik *et al.* (2006, p. 359) declare that "Groups of neurons interact to code information about the stimuli". The passage clarifies if the word "neurons" is replaced by the phrase "graduate students or postdocs". Chechik *et al.* (2006, p. 359) further state that "Neurons at higher processing stations may become largely independent to allow for easier readout". Now replace "neurons at higher" by "laboratory staff at". Chechik *et al.* (2006) are echoed by Ciocchi *et al.* (2015, p. 560), who state that some particular part of the brain "computes diverse information" and then sends "computations transmitted [*sic*]" to various brain "targets". Imagine now replacing brain by "laboratory staff" and "brain targets" by "assistants".

Figure 4 schematizes the reality of "reading" and "decoding".

The anthropomorphized neuron that performs "decoding" effectively becomes all of society, all "observers". Figure 5 shows this relation. The experimenter/observer is not separable operationally from the greater collective of observers that is the laboratory personnel. The laboratory, likewise, is not operationally separable from the greater society in which it is embedded. When the neuron is cast as "observer", it effectively becomes the universe of humans surrounding itself.

7.2 Why "decode" at all?

Like many, Zhang *et al.* (1998, p. 1037) ponder "which reconstruction algorithm is actually used by the biological system". Like many, however, they avoid pondering an even more important question, namely, why *any* reconstruction algorithm "is actually used by the biological system". Poor writing in the literature makes things worse. Consider, altogether, the following passage:

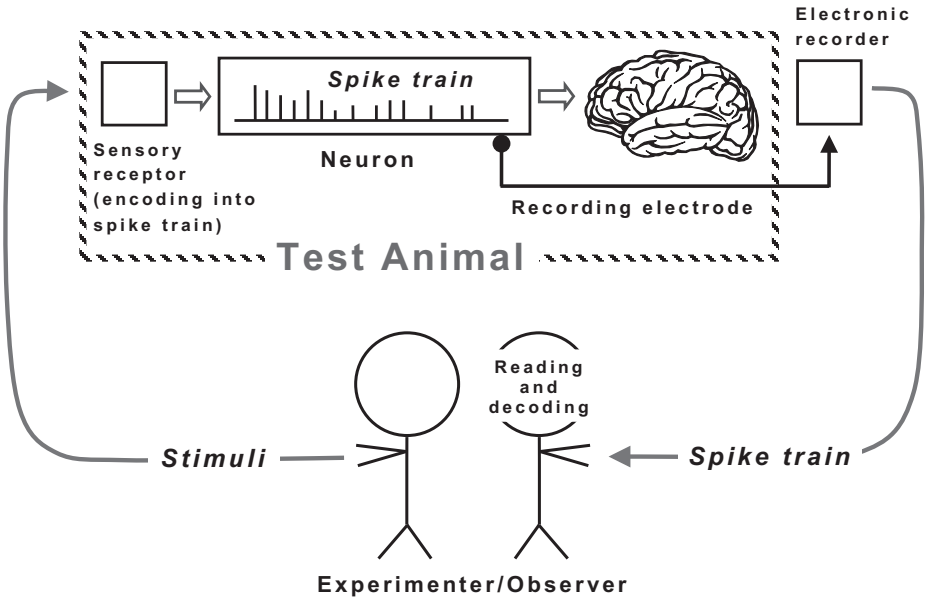

Figure 4.
The reality of "reading" and "decoding" (compare to Figures 1 and 3)

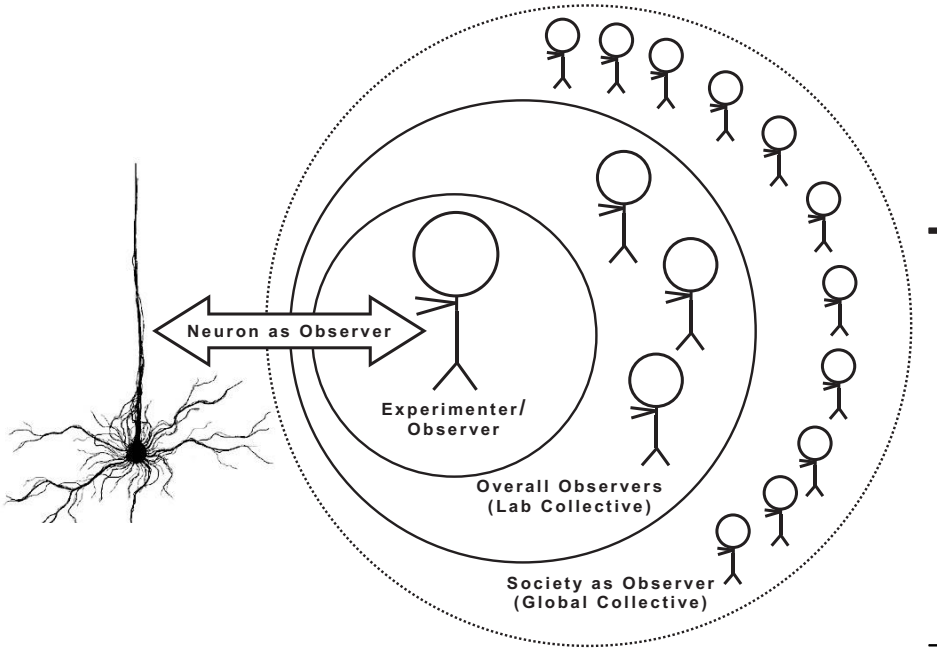

Figure 5. The neuron as the collective: the neuron as an observer (the two-sided arrow indicates "equivalence") and hence as the collectives that are the observer

> Of course, we do not consider the role of the visual system in general as being to reconstruct the image in the brain. Rather, this reconstruction [i.e. in the laboratory] should be seen as a form of benchmark – a test of the potential of a particular code (van Rullen and Thorpe, 2001, p. 1257).

Note well the vagueness of "image". Is it the actual perceived object or the percept in the mind, i.e. the "seeing" of the object? The first choice amounts to the actual *generation* of the stimulus by the looking organism, which is altogether ludicrous (to everyone except Kenneth Howard Norwich; as described in Nizami, 2009 and Winer *et al.*, 2002). However, if "image" refers to the percept, which is what the brain has already "constructed", then why "reconstruct" it?

To-date, there is no empirical evidence that the brain "decodes" anything, *or that it even needs to* (Nizami, 2014, 2015a). As Naka and Sakai (1993, p. 79) state, with respect to their animal research subject and the manner in which they (and others) have quantified retinal spike trains, "The catfish has no notion of 'multiplexed signals' or of 'cross-correlation'; these notions are ours". If, indeed, reconstruction refers to the computations done by the experimenters, how is the experimenters' evaluation of "the potential of a particular code" (van Rullen and Thorpe, 2001, p. 1257) even relevant? In fact, the experimenter's "estimation" (see above) provides a stimulus *identity/categorization* (e.g. "green Granny Smith apple") from the experimenter's list of given stimuli. But this is not the experienced percept (the internal picture that we call "apple"), and as such, it is of no use to anyone besides the experimenter.

"Decoding" has, since the time of Lettvin *et al.* (1959), become inseparable from the notion of "information processing". This is evident in many of the papers cited up to this juncture. Recall Bialek *et al.*'s (1991) statement (Section 6.2 above) that "All of an organism's *information* about the sensory world comes from real-time observation of the activity of its

own neurons" (italics supplied). The following section explains why "information processing" mandated "decoding". These details need to be aired because neuroscientists have not been forthcoming on this issue.

8. The "informative" neuron

8.1 Information Theory as used by neuroscientists

Neuroscientists use Shannon Information Theory to quantify "the ability of [physiological sensory] receptors (or other signal-processing elements) to transmit information about stimulus parameters" (Smith *et al.*, 1983, p. 82). For the unfamiliar reader, a brief recapitulation of Shannon Information Theory and its use in neurophysiology is appropriate, as follows. Shannon himself (Shannon, 1948) did not deal with neurons but rather with a "general communication system" which includes "An *information source* which produces a message or sequence of messages to be communicated to the receiving terminal" (original italics). The sent messages are groups of symbols, such as letters arranged into words and then into sentences (Shannon, 1948). The "general communication system" contains an encoder (the Transmitter), subsequent to the Information Source, and a later *decoder* (the Receiver). A symbol received is from the set of symbols that can be sent. Transmission is imperfect; not all symbols are received as they were sent. Information Transmitted can be computed after the transmission is complete, by knowing what symbols "k" (Events) were sent, what symbols "j" (Outcomes) were received, and how many times a "k" was received as a "j". The latter frequencies, called N_{jk}, can be arranged in two dimensions as a so-called "confusion matrix". Figure 6 shows the *communication engineers'* confusion matrix (Shannon, 1948).

Neuroscientists, too, use a confusion matrix in computing Information Transmitted. But their matrix differs somewhat from Shannon's, as will be described. First, note the rationale behind neuroscientists' use of Information Theory. During a sensory stimulus, a responsive neuron fires a train of voltage spikes. Each application of the *same* stimulus can evoke a *different* spike train, making the neuron's response to the stimulus look "confused". This in turn would cause the value of Information Transmitted to be less than its possible maximum, but it would nonetheless exceed zero, because the neuronal spike train has some measurable characteristics that are observed to change systematically with change in some

	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 6.
The communication engineers' confusion matrix, whose rows and columns have the same labels (compare to Figure 7)

property of the stimulus, such as physical intensity. The most popular of the *spike-train* measures is the mean stimulus-evoked spike *count*, taken over a sub-interval of the duration of the stimulus (right up to the full stimulus duration). There are other spike-train measures used for computation of Information Transmitted, such as the latency of the first stimulus-evoked spike (Furukawa and Middlebrooks, 2002; Nelken *et al.*, 2005; Saal *et al.*, 2009) or the interspike intervals (Lu and Wang, 2004) or "the principal components of the temporal waveform of the response" (Optican and Richmond, 1987, p. 168; also McClurkin *et al.*, 1991; Tovée *et al.*, 1993; Tovée and Rolls, 1995; Rolls *et al.*, 1996).

Regarding the construction of the neuroscientists' confusion matrix, Werner and Mountcastle (1965) provide the archetype. Their spike-train measure is taken as Shannon's "Outcome" in response to the stimulus, and the stimulus is labelled as Shannon's "Event" according to whatever measurable stimulus property is being varied, such as the intensity. In Werner and Mountcastle (1965), the Events are in fact called *stimulus categories*, which can (in practice) be *ranges* of the stimulus property in question. Likewise, the Outcomes are in fact called *response categories*, and are *always* ranges of the used spike-train measure (e.g. total count of evoked voltage-spikes). Figure 7 shows the neuroscientists' confusion matrix (after Werner and Mountcastle, 1965, p. 387). Contrast all of this to Shannon (1948), who specifies that each Event is from a limited set of distinct things (such as symbols), each evoking an Outcome that is one of the possible Events. But Werner and Mountcastle (1965) and their successors interpret Events as elements of a continuum, such as stimulus intensity; they likewise take Outcomes as magnitudes of a *different* continuum, one that describes a neuron's response to the stimulus, such as spike count. Altogether, the Werner-Mountcastle interpretation produces an Information Transmitted whose meaning is unclear, and which therefore is unlikely to be the actual Information Transmitted (Nizami, 2012, 2014). This conclusion, which arises from the particulars of the *computations*, applies equally well regardless of the used spike-train measure.

The vagueness of the Werner-Mountcastle interpretation of Information Transmitted is a fatal flaw. Neuroscientists fail to see this.

Some assemble the confusion matrix by working backwards to *infer* whichever Event evoked each particular neuronal Outcome, using a *decoder* (presumed to be used by the

	Stimulus category (Event)						
Spike-count category (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}	$N_{2.}$
-	-	-	-	-	-	-	-
i	N_{i1}	N_{i2}	-	N_{ik}	-	N_{in}	$N_{i.}$
-	-	-	-	-	-	-	-
n	N_{n1}	N_{n2}	-	N_{nk}	-	N_{nn}	$N_{n.}$
Column totals	$N_{.1}$	$N_{.2}$	-	$N_{.k}$	-	$N_{.n}$	Sum $= N$

Figure 7. The neuroscientists' confusion matrix, whose rows and columns have different labels from each other (compare to Figure 6)

brain) that "receives a spike train as input and guesses which stimulus evoked the spike train" (Nelken *et al.*, 2005, p. 200; see also Georgopoulos and Massey, 1988; Rieke *et al.*, 1995; Roddey and Jacobs, 1996; Warland *et al.*, 1997; Buračas *et al.*, 1998; Furukawa and Middlebrooks, 2002; Averbeck *et al.*, 2003; Passaglia and Troy, 2004; DiCaprio *et al.*, 2007; Sadeghi *et al.*, 2007; Lawhern *et al.*, 2011; So *et al.*, 2012). Unfortunately, as noted in Section 7 above, such decoding is essentially guesswork. And even if it were error-free, the computed Information Transmitted would still be unclear, thanks to the aforementioned departures of the Werner-Mountcastle method from Shannon's (1948) original computations.

8.2 "A neural system that could carry out categorization followed by specific identification": Sugase and colleagues

Sugase *et al.* (1999 [670+ citations]) introduce their work by stating that "Information Theory was used to investigate how well the neuronal responses could categorize the stimuli" (Sugase *et al.*, 1999, p. 869). They then perform various classic Werner-Mountcastle computations of Information Transmitted, following many Werner-Mountcastle-style assumptions about what constitute "stimuli" and "neuronal responses" and so forth. They then conclude (Werner and Mountcastle, 1965, p. 872) that "Our result demonstrates a physiological precursor for a neural system that could carry out categorization followed by specific identification". The term "physiological precursor" presumably constitutes the neuronal spike trains evoked by their stimuli. However, the "neural system that could carry out categorization followed by specific identification" is proposed without any correlates from physiology, and in fact constitutes Sugase *et al.* themselves, who carry out the categorization to compute Information Transmitted, followed by the "specific identification" to infer the stimulus, i.e. to do "decoding". And 15 years later, in Sugase-Miyamoto *et al.* (2014), two of the original four authors of Sugase *et al.* (1999) join with two new co-authors to provide similar experiments, followed by similarly-mistaken claims.

The notion that a neuron's response to the stimulus is "confused", hence amenable to Information Theory, is another way of saying that the neuron is "uncertain". Loss of uncertainty is, in Information Theory, gain of information (Shannon, 1948) – or, as some neuroscientists interpret it, a gain of knowledge, as follows.

9. The conscious, "knowing" neuron and its alternative, *emergence*

9.1 The neuron, conscious and knowing but alone and uncertain

As represented in the Bialek *et al.* (1991) quotation (Section 6.2 above) about "real-time observation of the activity of its own neurons", neuroscientists imagine that the observer of neuronal spike trains is *another neuron*. Such an "observer neuron" is presumably conscious. It is also sometimes "ideal", insofar as it achieves the best detection or discrimination of stimuli that *mathematics* allows. In short, the neuron becomes a mathematician, thanks to an algebraically convenient set of assumptions, offered within Signal Detection Theory (SDT) (Green and Swets, 1966/1988). SDT is used by Geisler *et al.* (1991), among many, who "apply an ideal-observer analysis to arbitrary discrimination stimuli [*sic*]", altogether involving "single neurons in discrimination tasks" (Geisler *et al.*, 1991, p. 335). Note well that the discriminations are *presumed* to be performed by single neurons, although small neural populations may serve also (for example, Deneve *et al.*, 1999 [370+ citations]; Seriès *et al.*, 2009). Of course, the actual SDT discriminations are done by laboratory personnel, who examine neuronal spike-trains with the aid of books and computers. Now, SDT is a statistical method, with which the sensory nervous system could be "assumed to have some uncertainty" (Geisler *et al.*, 1991, p. 335) – uncertainty about what stimuli were available and at what probabilities of appearance, just as in neuroscientists' use of

Information Theory (Section 8). Geisler *et al.* (1991, p. 344) declare that, therefore, "later neurons in the sensory system might have *implicit knowledge*" (italics supplied). Or, as stated by SDT enthusiasts Gold and Shadlen (2001 [760+ citations]), neurons in "brain structures involved in planning for action" (and therefore influenced by sensory input) are "affected by knowledge of prior probabilities and expectation of reward in decision-making" (Gold and Shadlen, 2001, p. 13). Such language is hardly rare; for some references, see Gold and Shadlen (2001).

The alleged "knowledgeable" decision-making neurons need not be at the brain. Hagins (1965, p. 405 [150+ citations]) presumes that a visual organ's photoreceptor-cell's synapse is "Operating as a decision-making device like some part of the retina [*sic*] or brain". That is, the retina of the eye "knows" (Atick and Redlich, 1992 [630+ citations]; see, for example, the "eye's mind" in Norwich, 1978, p. 162). Of course, this doctrine has an obvious flaw: if the sort of neurons in question are not at the brain, then the brain is redundant to the function in question, that is, it has nothing to do (as noted by Ashby, 1995, among others).

9.2 Emergence

Neuroscientists' assignment of consciousness to individual neurons is Reductionist. And it fails. The Reductionist approach describes the mind in terms of distinct pieces rather than as something that arises from a much larger number of points working simultaneously as a coordinated system. But there is hope in the latter concept, called *emergence*, which relates to self-organization (von der Malsburg, 1997; Chapters 6, 23, and 24 of Ramage and Shipp, 2009). As John (1976, p. 1) declares (original italics, and original internal quotation marks):

> I believe that "mind", under which rubric are subsumed such phenomena as consciousness, subjective experience, the concept of self, and self-awareness, is an *emergent property* of sufficiently complex and appropriately organized matter.

In other words, 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.

MacKay and McCulloch (1952, p. 135) presage "emergence" in the course of expressing some last words on "information": "If cerebral activity is the stochastic process it appears to be [i.e. incorporating some inherent randomness], [then] the informationally significant descriptive concepts when once discovered seem likely to have as much relation to the parameters defining the states of individual neurons, as concepts such as entropy and temperature have to the motions of individual gas molecules – and little more".

Let us assume that individual neurons need not mutually *describe* – i.e. that they need not be conscious – to interact. Neurons need *not* be military generals, detectives, informants, journalists, grandmothers, messengers, marketers or signalmen. Single-neuron consciousness had been implied by Lettvin *et al.* (1959) and his successors, who could not believe that consciousness could emerge from non-consciousness – for example, that consciousness emerges at the larger scale; that mind *emerges* in brain.

10. Anthropomorphization as Reductionism

Anthropomorphization is a form of Reductionism. Reductionism is the attempt to explain a complicated behavior or action, emanating from a complicated mechanism, in terms of simpler behaviors or actions, emanating from simpler mechanisms. Reductionism gives us a

doctrine: that the stimulus-evoked voltage-spike trains of single neurons, perhaps even those neurons that are physiologically peripheral, are all that is needed to account for all sensory relations associated with the stimuli. Examples of peripheral neurons are the primary sensory afferents, with their attached sensory receptor cell(s); examples of such sensory relations are the "Psychophysical Laws"; and examples of the presumptive linking of the two can be found in Zwislocki (2009), for hearing-science. The ongoing presumption, i.e. that psychophysical laws derive from single primary sensory afferents alone, represents a remarkably narrow "neural Reductionism", which provides nothing for sensory neurons further brain-wards to do (Ashby, 1995).

There were contemporaries of Lettvin *et al.* (1959) who warned against attempting to understand sensations through single-neuron-centered mathematical *modeling*, such as schemes for encoding and decoding. For example, Rapoport (1956, p. 315) pointed out "the prodigious gap between the conceptual "nervous systems" of mathematicians and engineers and the real nervous tissue of the physiologist" (original internal quotation marks). That gap remains prodigious after 60 years. Walter and Gardiner (1970, p. 347) repeated the warnings (original italics):

> It is important to emphasize the need to distinguish conceptually between the coding hypothesized to be operating *within* an information processing system, and the coding which we, as observers, choose to use in measuring and describing that system.

Note well the recognition of *observer*. What Walter and Gardiner call the "information processing system" is, to them, the test animal, in particular its sensory system(s) which connect the outside world to its brain. Walter and Gardiner (1970, p. 353) further admonish us, "This distinction between a variable which is informative to us as observers, according to a coding scheme which we develop, and a variable which can be hypothesized to be informative to the animal, but perhaps with an unknown coding scheme, is a distinction to be borne in mind continuously". Clearly, that distinction has been lost.

11. Summary and conclusions

For more than half a century, neuroscientists have granted neurons the ability to decide, judge, recognize, categorize, detect, distinguish and/or discriminate. Neurons have been military generals, detectives, informants, journalists, grandmothers, messengers, marketers or signalmen, among other roles.

All of this is *anthropomorphization*. It arose because single neurons were cast as "observers" who "estimate" the stimulus by means of "decoding". Decoding is the mathematical reduction of the stimulus-evoked spike trains to the particular stimuli inferred to elicit them. Without these algorithmically-generated "guesses", there is allegedly no perception. Of course, perception is not guesswork, and there is no evidence or justification for "decoding". Indeed, the observer is the neuroscientist not the neuron.

Interpreting neurons as "observers" endows neurons with consciousness. This weakens any impetus to find credible *multi-neuron* theories of consciousness itself. The single-neuron Reductionist view has resulted in wasted time, wasted money and wasted resources. Reductionism itself will continue to hinder progress in understanding the sensory nervous system inside and outside of the brain, and the roles of the sensory nervous system and the brain in cognition. There is an alternative: abandon Reductionism. This will free the time and money needed to pursue holistic approaches, for example, treating consciousness as "emergent".

References

Aldworth, Z.N., Bender, J.A. and Miller, J.P. (2012), "Information transmission in cercal giant interneurons is unaffected by axonal conduction noise", *PLoS ONE*, Vol. 7 No. 1, pp. 1-10.

Alkasab, T.K., Bozza, T.C., Cleland, T.A., Dorries, K.M., Pearce, T.C., White, J. and Kauer, J.S. (1999), "Characterizing complex chemosensors: information-theoretic analysis of olfactory systems", *TINS*, Vol. 22 No. 3, pp. 102-108.

Arabzadeh, E., Panzeri, S. and Diamond, M.E. (2004), "Whisker vibration information carried by rat barrel cortex neurons", *Journal of Neuroscience*, Vol. 24 No. 26, pp. 6011-6020.

Arabzadeh, E., Panzeri, S. and Diamond, M.E. (2006), "Deciphering the spike train of a sensory neuron: counts and temporal patterns in the rat whisker pathway", *Journal of Neuroscience*, Vol. 26 No. 36, pp. 9216-9226.

Ashby, F.G. (1995), "Resurrecting Information Theory: information, sensation, and perception by Kenneth H. Norwich", *American Journal of Psychology*, Vol. 108, pp. 609-614.

Atick, J.J. and Redlich, A.N. (1990), "Towards a theory of early visual processing", *Neural Computation*, Vol. 2 No. 3, pp. 308-320.

Atick, J.J. and Redlich, A.N. (1992), "What does the retina know about natural scenes?", *Neural Computation*, Vol. 4 No. 2, pp. 196-210.

Averbeck, B.B., Crowe, D.A., Chafee, M.V. and Georgopoulos, A.P. (2003), "Neural activity in prefrontal cortex during copying geometrical shapes II. Decoding shape segments from neural ensembles", *Experimental Brain Research*, Vol. 150 No. 2, pp. 142-153.

Baddeley, R. (2000/2008), "Introductory Information Theory and the brain", in Baddeley, R., Hancock, P. and Földiák, P. (Eds), *Information Theory and the Brain*, Cambridge University Press, New York, NY, pp. 1-19.

Barlow, H.B. (1994), "The neuron doctrine in perception", in Gazzaniga, M. (Ed.), *The Cognitive Neurosciences*, MIT Press, Cambridge, MA, pp. 415-435.

Bialek, W., Rieke, F., de Ruyter van Steveninck, R.R. and Warland, D. (1991), "Reading a neural code", *Science*, Vol. 252 No. 5014, pp. 1854-1857.

Bullock, T.H. (1961), "The problem of recognition in an analyzer made of neurons", in Rosenblith, W.A. (Ed.), *Sensory Communication*, MIT Press, Cambridge, MA, pp. 717-724.

Buračas, G.T., Zador, A.M., DeWeese, M.R. and Albright, T.D. (1998), "Efficient discrimination of temporal patterns by motion-sensitive neurons in primate visual cortex", *Neuron*, Vol. 20 No. 5, pp. 959-969.

Burton, B.G. (2000/2008), "Problems and solutions in early visual processing", in Baddeley, R., Hancock, P. and Földiák, P. (Eds), *Information Theory and the Brain*, Cambridge University Press, New York, NY, pp. 25-40.

Chacron, M.J., Longtin, A. and Maler, L. (2003), "The effects of spontaneous activity, background noise, and the stimulus ensemble on information transfer in neurons", *Network*, Vol. 14 No. 4, pp. 803-824.

Chechik, G., Anderson, M.J., Bar-Yosef, O., Young, E.D., Tishby, N. and Nelken, I. (2006), "Reduction of information redundancy in the ascending auditory pathway", *Neuron*, Vol. 51 No. 3, pp. 359-368.

Ciocchi, S., Passecker, J., Malagon-Vina, H., Mikus, N. and Klausberger, T. (2015), "Selective information routing by ventral hippocampal CA1 projection neurons", *Science*, Vol. 348 No. 6234, pp. 560-563.

Crick, F. and Koch, C. (2003), "A framework for consciousness", *Nature Neuroscience*, Vol. 6 No. 2, pp. 119-126.

Darian-Smith, I., Rowe, M.J. and Sessle, B.J. (1968), "'Tactile' stimulus intensity: information transmission by relay neurons in different trigeminal nuclei", *Science*, Vol. 160 No. 3829, pp. 791-794.

Deneve, S., Latham, P.E. and Pouget, A. (1999), "Reading population codes: a neural implementation of ideal observers", *Nature Neuroscience*, Vol. 2 No. 8, pp. 740-745.

DiCaprio, R.A., Billimoria, C.P. and Ludwar, B.C. (2007), "Information rate and spike-timing precision of proprioceptive afferents", *Journal of Neurophysiology*, Vol. 98 No. 3, pp. 1706-1717.

Estebanez, L., El Boustani, S., Destexhe, A. and Shulz, D.E. (2014), "Ce que les vibresses disent au cerveau tactile [what the whiskers tell the tactile brain]", *Médecine/Sciences*, Paris, Vol. 30 No. 1, pp. 93-98.

Faghihi, F., Kolodziejski, C., Fiala, A., Wörgötter, F. and Tetzlaff, C. (2013), "An information theoretic model of information processing in the Drosophila olfactory system: the role of inhibitory neurons for system efficiency", *Frontiers in Computational Neuroscience*, Vol. 7 No. 183, pp. 1-8.

Furukawa, S. and Middlebrooks, J.C. (2002), "Cortical representation of auditory space: information-bearing features of spike patterns", *Journal of Neurophysiology*, Vol. 87 No. 4, pp. 1749-1762.

Gehr, D.D., Komiya, H. and Eggermont, J.J. (2000), "Neuronal responses in cat primary auditory cortex to natural and altered species-specific calls", *Hearing Research*, Vol. 150 Nos 1/2, pp. 27-42.

Geisler, W.S., Albrecht, D.G., Salvi, R.J. and Saunders, S.S. (1991), "Discrimination performance of single neurons: rate and temporal-pattern information", *Journal of Neurophysiology*, Vol. 66, pp. 334-362.

Georgopoulos, A.P. and Massey, J.T. (1988), "Cognitive spatial-motor processes. 2. Information transmitted by the direction of two-dimensional arm movements and by neuronal populations in primate motor cortex and area 5", *Experimental Brain Research*, Vol. 69, pp. 315-326.

Gnadt, J.W. and Breznen, B. (1996), "Statistical analysis of the information content in the activity of cortical neurons", *Vision Research*, Vol. 36 No. 21, pp. 3525-3537.

Gochin, P.M., Colombo, M., Dorfman, G.A., Gerstein, G.L. and Gross, C.G. (1994), "Neural ensemble coding in inferior temporal cortex", *Journal of Neurophysiology*, Vol. 71, pp. 2325-2337.

Gold, J.I. and Shadlen, M.N. (2001), "Neural computations that underlie decisions about sensory stimuli", *Trends in Cognitive Sciences*, Vol. 5 No. 1, pp. 10-16.

Golomb, D., Kleinfeld, D., Reid, R.C., Shapley, R.M. and Shraiman, B.I. (1994), "On temporal codes and the spatiotemporal response of neurons in the lateral geniculate nucleus", *Journal of Neurophysiology*, Vol. 72, pp. 2990-3003.

Green, D.M. and Swets, J.A. (1966/1988), *Signal Detection Theory and Psychophysics*, Peninsula Publishing, Los Altos, CA.

Gütig, R. (2016), "Spiking neurons can discover predictive features by aggregate-label learning", *Science*, Vol. 351 No. 6277, p. 1041.

Hagins, W.A. (1965), "Electrical signs of information flow in photoreceptors", *Cold Spring Harbor Symposia on Quantitative Biology*, Vol. 30, pp. 403-418.

Hannam, A.G. and Farnsworth, T.J. (1977), "Information transmission in trigeminal mechanosensitive afferents from teeth in the cat", *Archives of Oral Biology*, Vol. 22 No. 3, pp. 181-186.

Heller, J., Hertz, J.A., Kjaer, T.W. and Richmond, B.J. (1995), "Information flow and temporal coding in primate pattern vision", *Journal of Computational Neuroscience*, Vol. 2 No. 3, pp. 175-193.

Humphrey, N.K. (1970), "What the frog's eye tells the monkey's brain", *Brain, Behavior and Evolution*, Vol. 3 Nos 1/4, pp. 324-337.

John, E.R. (1976), "A model of consciousness", in Schwartz, G.E. and Shapiro, D. (Eds), *Consciousness and Self-Regulation*, Springer, Plenum Press, New York, NY, pp. 1-50.

Kenton, B. and Kruger, L. (1971), "Information transmission in slowly adapting mechanoreceptor fibers", *Experimental Neurology*, Vol. 31 No. 1, pp. 114-139.

Koch, K., McLean, J., Segev, R., Freed, M.A., Berry II, M.J., Balasubramanian, V. and Sterling, P. (2006), "How much the eye tells the brain", *Current Biology*, Vol. 16 No. 14, pp. 1428-1434.

Lass, Y. and Abeles, M. (1975), "Transmission of information by the axon: I. Noise and memory in the myelinated nerve fiber of the frog", *Biological Cybernetics*, Vol. 19 No. 2, pp. 61-67.

Lawhern, V., Nikonov, A.A., Wu, W. and Contreras, R.J. (2011), "Spike rate and spike timing contributions to coding taste quality information in rat periphery", *Frontiers in Integrative Neuroscience*, Vol. 5 No. 18, pp. 1-14.

Lettvin, J.Y., Maturana, H.R., McCulloch, W.S. and Pitts, W.H. (1959), "What the frog's eye tells the frog's brain", *Proceedings of the Institute of Radio Engineers*, Vol. 47 No. 11, pp. 1940-1951.

Lu, T. and Wang, X. (2004), "Information content of auditory cortical responses to time-varying acoustic stimuli", *Journal of Neurophysiology*, Vol. 91 No. 1, pp. 301-313.

MacKay, D.M. and McCulloch, W.S. (1952), "The limiting information capacity of a neuronal link", *Bulletin of Mathematical Biophysics*, Vol. 14 No. 2, pp. 127-135.

MacLeod, K., Bäcker, A. and Laurent, G. (1998), "Who reads temporal information contained across synchronized and oscillatory spike trains?", *Nature*, Vol. 395 No. 6703, pp. 693-698.

McClurkin, J.W., Optican, L.M., Richmond, B.J. and Gawne, T.J. (1991), "Concurrent processing and complexity of temporally encoded neuronal messages in visual perception", *Science*, Vol. 253, pp. 675-677.

Machens, C.K., Schütze, H., Franz, A., Kolesnikova, O., Stemmler, M.B., Ronacher, B. and Herz, A.V.M. (2003), "Single auditory neurons rapidly discriminate conspecific communication signals", *Nature Neuroscience*, Vol. 6 No. 4, pp. 341-342.

Miller, J.H. (2015), *A Crude Look at the Whole*, Basic, New York, NY.

Naka, K. and Sakai, H.M. (1993), "Can we ever understand how the retina communicates with the brain?", in Shapley, R. and Lam, D.M.-K. (Eds), *Contrast Sensitivity*, MIT Press, Cambridge, MA, pp. 75-81.

Nelken, I., Chechik, G., Mrsic-Flogel, T.D., King, A.J. and Schnupp, J.W.H. (2005), "Encoding stimulus information by spike numbers and mean response time in primary auditory cortex", *Journal of Computational Neuroscience*, Vol. 19 No. 2, pp. 199-221.

Nizami, L. (2002), "Estimating auditory neuronal dynamic range using a fitted function", *Hearing Research*, Vol. 167 Nos 1/2, pp. 13-27.

Nizami, L. (2003), "Afferent response parameters derived from postmasker probe-detection thresholds: 'the decay of sensation' revisited", *Hearing Research*, Vol. 175 Nos 1/2, pp. 14-35.

Nizami, L. (2005a), "Dynamic range relations for auditory primary afferents", *Hearing Research*, Vol. 208 Nos 1-2, pp. 26-46.

Nizami, L. (2005b), "Intensity-difference limens predicted from the click-evoked peripheral N_1: the mid-level hump and its implications for intensity encoding", *Mathematical Biosciences*, Vol. 197, pp. 15-34.

Nizami, L. (2009), "Sensory systems as cybernetic systems that require awareness of alternatives to interact with the world: analysis of the brain-receptor loop in Norwich's Entropy Theory of Perception", *Proceedings of the 2009 IEEE International Conference on Systems, Man, and Cybernetics, San Antonio, TX*, pp. 3477-3482.

Nizami, L. (2012), "Confusing the 'confusion matrix': the misapplication of Shannon Information Theory in sensory psychology", *Acta Systemica (International Journal of the International Institute for Advanced Studies in Systems Research and Cybernetics)*, Vol. 12, pp. 1-17.

Nizami, L. (2014), "Information Theory's failure in neuroscience: on the limitations of cybernetics", Paper No. 158, *Proceedings of the IEEE 2014 Conference on Norbert Wiener in the 21st Century, IEEE, Piscataway, NJ*.

Nizami, L. (2015a), "Homunculus strides again: why 'information transmitted' in neuroscience tells us nothing", *Kybernetes*, Vol. 44, pp. 1358-1370.

Nizami, L. (2015b), "Flaws in loudness standard ANSI S3.4-2007: the derivation of nonzero sensation at absolute detection threshold is circular" Paper 38, *INTER-NOISE and NOISE-CON Congress and Conference Proceedings, Institute of Noise Control Engineering*, Vol. 250 No. 6.

Nizami, L. and Schneider, B.A. (1997), "Auditory dynamic range derived from the mean rate-intensity function in the cat", *Mathematical Biosciences*, Vol. 141 No. 1, pp. 1-28.

Nizami, L. and Schneider, B.A. (2000), "The periodicity of forward-masked auditory pip-detection thresholds, predicted from the output power of the auditory filter during ringing", *Hearing Research*, Vol. 144 Nos 1/2, pp. 168-174.

Norwich, K.H. (1978), "An hypothesis on information, memory and perception", *Medical Hypotheses*, Vol. 4 No. 2, pp. 156-164.

Optican, L.M. and Richmond, B.J. (1987), "Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex III. Information theoretic analysis", *Journal of Neurophysiology*, Vol. 57, pp. 162-178.

Osborne, L.C., Bialek, W. and Lisberger, S.G. (2004), "Time course of information about motion direction in visual area MT of macaque monkeys", *Journal of Neuroscience*, Vol. 24 No. 13, pp. 3210-3222.

Passaglia, C.L. and Troy, J.B. (2004), "Information transmission rates of cat retinal ganglion cells", *Journal of Neurophysiology*, Vol. 91, pp. 1217-1229.

Ramage, M. and Shipp, K. (2009), *Systems Thinkers*, Springer, New York, NY.

Rapoport, A. (1956), "Three symposia (Parts 1 and 2: pp. 303-315)", *Behavioral Science*, Vol. 1, pp. 303-326.

Restrepo, D. (2004), "What the frog's nose tells the frog's brain", *Journal of General Physiology*, Vol. 123 No. 2, pp. 97-98.

Rieke, F., Bodnar, D.A. and Bialek, W. (1995), "Naturalistic stimuli increase the rate and efficiency of information transmission by primary auditory afferents", *Proceedings of the Royal Society of London, Series B*, Vol. 262 No. 1365, pp. 259-265.

Rieke, F., Warland, D., de Ruyter van Steveninck, R. and Bialek, W. (1997), *Spikes: Exploring the Neural Code*, MIT Press, Cambridge, MA.

Roddey, J.C. and Jacobs, G.A. (1996), "Information theoretic analysis of dynamical encoding by filiform mechanoreceptors in the cricket cercal system", *Journal of Neurophysiology*, Vol. 75, pp. 1365-1376.

Rogers, R.F., Runyan, J.D., Vaidyanathan, A.G. and Schwaber, J.S. (2001), "Information theoretic analysis of pulmonary stretch receptor spike trains", *Journal of Neuroscience*, Vol. 85, pp. 448-461.

Rolls, E.T., Critchley, H.D. and Treves, A. (1996), "Representation of olfactory information in the primate orbitofrontal cortex", *Journal of Neurophysiology*, Vol. 75 No. 5, pp. 1982-1996.

Rolls, E.T., Critchley, H.D., Verhagen, J.V. and Kadohisa, M. (2010), "The representation of information about taste and odor in the orbitofrontal cortex", *Chemosensory Perception*, Vol. 3 No. 1, pp. 16-33.

Saal, H.P., Vijayakumar, S. and Johansson, R.S. (2009), "Information about complex fingertip parameters in individual human tactile afferent neurons", *Journal of Neuroscience*, Vol. 29 No. 25, pp. 8022-8031.

Sadeghi, S.G., Chacron, M.J., Taylor, M.C. and Cullen, K.E. (2007), "Neural variability, detection thresholds, and information transmission in the vestibular system", *Journal of Neuroscience*, Vol. 27 No. 4, pp. 771-781.

Seriès, P., Stocker, A.A. and Simoncelli, E.P. (2009), "Is the homunculus 'aware' of sensory adaptation?", *Neural Computation*, Vol. 21 No. 12, pp. 3271-3304.

Shannon, C.E. (1948), "A mathematical theory of communication", *Bell System Technical Journal*, Vol. 27 No. 4, pp. 623-656.

Skaggs, W.E., McNaughton, B.L., Gothard, K.M. and Markus, E.J. (1992), "An information-theoretic approach to deciphering the hippocampal code", in Hanson, S.J., Cowan, J.D. and Giles, C.L. (Eds), *Advances in Neural Information Processing Systems 5 (NIPS 1992)*, Morgan Kaufmann, pp. 1030-1037.

Smith, D.V., Bowdan, E. and Dethier, V.G. (1983), "Information transmission in tarsal sugar receptors of the blowfly", *Chemical Senses*, Vol. 8 No. 1, pp. 81-101.

So, K., Ganguly, K., Jimenez, J., Gastpar, M.C. and Carmena, J.M. (2012), "Redundant information encoding in primary motor cortex during natural and prosthetic motor control", *Journal of Computational Neuroscience*, Vol. 32 No. 3, pp. 555-561.

Stein, R.B. (1967), "The information capacity of nerve cells using a frequency code", *Biophysical Journal*, Vol. 7 No. 6, pp. 797-826.

Sugase-Miyamoto, Y., Matsumoto, N., Ohyama, K. and Kawano, K. (2014), "Face inversion decreased information about facial identity and expression in face-responsive neurons in macaque area TE", *Journal of Neuroscience*, Vol. 34 No. 37, pp. 12457-12469.

Sugase, Y., Yamane, S., Ueno, S. and Kawano, K. (1999), "Global and fine information coded by single neurons in the temporal visual cortex", *Nature*, Vol. 400 No. 6747, pp. 869-873.

Tolhurst, D.J. (1989), "The amount of information transmitted about contrast by neurones in the cat's visual cortex", *Visual Neuroscience*, Vol. 2 No. 4, pp. 409-413.

Tovée, M.J. and Rolls, E.T. (1995), "Information encoding in short firing rate epochs by single neurons in the primate temporal visual cortex", *Visual Cognition*, Vol. 2 No. 1, pp. 35-58.

Tovée, M.J., Rolls, E.T., Treves, A. and Bellis, R.P. (1993), "Information encoding and the responses of single neurons in the primate temporal visual cortex", *Journal of Neurophysiology*, Vol. 70, pp. 640-654.

van Rullen, R. and Thorpe, S.J. (2001), "Rate coding versus temporal order coding: what the retinal ganglion cells tell the visual cortex", *Neural Computation*, Vol. 13 No. 6, pp. 1255-1283.

Victor, J.D. (2006), "Approaches to information-theoretic analysis of neural activity", *Biological Theory*, Vol. 1 No. 3, pp. 302-316.

von der Malsburg, C. (1997), "The coherence definition of consciousness", in Ito, M., Miyashita, Y. and Rolls, E.T. (Eds), *Cognition, Computation, and Consciousness*, Oxford University Press, New York, NY, pp. 193-204.

Walløe, L. (1970), "On the transmission of information through sensory neurons", *Biophysical Journal*, Vol. 10 No. 8, pp. 745-763.

Walter, D.O. and Gardiner, M.F. (1970), "Some guidelines from system science for studying neural information processing", *International Review of Neurobiology*, Vol. 13, pp. 343-374.

Warland, D.K., Reinagel, P. and Meister, M. (1997), "Decoding visual information from a population of retinal ganglion cells", *Journal of Neurophysiology*, Vol. 78 No. 5, pp. 2336-2350.

Weisstein, N. (1969), "What the frog's eye tells the human brain: single cell analyzers in the human visual system", *Psychological Bulletin*, Vol. 72 No. 3, pp. 157-176.

Werner, G. and Mountcastle, V.B. (1965), "Neural activity in mechanoreceptive cutaneous afferents: stimulus-response relations, Weber functions, and information transmission", *Journal of Neurophysiology*, Vol. 28, pp. 359-397.

Wiener, M.C., Oram, M.W., Liu, Z. and Richmond, B.J. (2001), "Consistency of encoding in monkey visual cortex", *Journal of Neuroscience*, Vol. 21 No. 20, pp. 8210-8221.

Winer, G.A., Cottrell, J.E., Gregg, V., Fournier, J.S. and Bica, L.A. (2002), "Fundamentally misunderstanding visual perception", *American Psychologist*, Vol. 57 Nos 6/7, pp. 417-424.

Zhang, K., Ginzburg, I., McNaughton, B.L. and Sejnowski, T.J. (1998), "Interpreting neuronal population activity by reconstruction: unified framework with application to hippocampal place cells", *Journal of Neurophysiology*, Vol. 79, pp. 1017-1044.

Zwislocki, J.J. (2009), *Sensory Neuroscience: Four Laws of Psychophysics*, Springer Science+Business Media, New York, NY.

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