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Homunculus strides again: why "information transmitted" in neuroscience tells us nothing

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Abstract

Purpose – For half a century, neuroscientists have used Shannon Information Theory to calculate "information transmitted," a hypothetical measure of how well neurons "discriminate" amongst stimuli. Neuroscientists' computations, however, fail to meet even the technical requirements for credibility. Ultimately, the reasons must be conceptual. That conclusion is confirmed here, with crucial implications for neuroscience. The paper aims to discuss these issues.
Design/methodology/approach – Shannon Information Theory depends upon a physical model, Shannon's "general communication system." Neuroscientists' interpretation of that model is scrutinized here.
Findings – In Shannon's system, a recipient receives a message composed of symbols. The symbols received, the symbols sent, and their hypothetical occurrence probabilities altogether allow calculation of "information transmitted." Significantly, Shannon's system's "reception" (decoding) side physically mirrors its "transmission" (encoding) side. However, neurons lack the "reception" side; neuroscientists nonetheless insisted that decoding must happen. They turned to Homunculus, an internal humanoid who infers stimuli from neuronal firing. However, Homunculus must contain a Homunculus, and so on ad infinitum – unless it is super-human. But any need for Homunculi, as in "theories of consciousness," is obviated if consciousness proves to be "emergent."
Research limitations/implications – Neuroscientists' "information transmitted" indicates, at best, how well neuroscientists themselves can use neuronal firing to discriminate amongst the stimuli given to the research animal.
Originality/value – A long-overdue examination unmasks a hidden element in neuroscientists' use of Shannon Information Theory, namely, Homunculus. Almost 50 years' worth of computations are recognized as irrelevant, mandating fresh approaches to understanding "discriminability."

Keywords Information theory, Brain, Homunculus, Neuron, Observer, Symmetry
Paper type Research paper

1. Introduction

In *Cybernetics*, Wiener (1961, p. vii) stated that "The role of information and the technique of measuring and transmitting information constitute a whole discipline for the engineer, for the neuroscientist, for the psychologist, and for the sociologist." Sociology aside, psychologists have, for 64 years, used the discrete summations from Shannon Information Theory (Shannon, 1948) to quantify "information transmitted" (Garner and Hake, 1951). The latter is presented in quotation marks to differentiate it from Shannon's own Information Transmitted, which is unambiguous (Nizami, 2010, 2011a, b, 2013). The maximum of psychologists' "information transmitted," the so-called "channel capacity," is actually memory capacity (Nizami, 2010, 2011a, b, 2013).

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However, Shannon's summations have also been used by neuroscientists, after Werner and Mountcastle (1965), to quantify the neuroscience version of "information transmitted," defined as "the ability of [physiological sensory] receptors (or other signal-processing elements) to transmit information about stimulus parameters" (Smith *et al.*, 1983, p. 82). Here "information transmitted" proves to be entirely uninformative, even if stimulus-evoked counts of neuronal voltage spikes can be worked backward to infer the hypothetical evoking stimuli – which is a probabilistic process (Nizami, 2014a). Neuroscientists' "information transmitted" nonetheless continues to influence cognitive science, making it deserving of long-overdue scrutiny. An unexamined core issue of the neuroscience approach is: how neuroscientists interpreted the model system underlying Shannon's Information Theory, his "general communication system." That scrutiny reveals that: Shannon himself missed a component inherent to his own system, the observer; neuroscientists in fact replaced the observer by Homunculus, an anthropomorphic entity within the animal's brain, to "decode" neuronal firing; Homunculus is an impossibility; and neuroscientists' "information transmitted" (and, by the same token, similar discrimination measures such as Signal Detection Theory *d′*; Green and Swets, 1966/1988) reveals, at best, how well neuroscientists themselves can (on average) discriminate among stimuli by using the animal's stimulus-evoked neuronal firing. Ultimately we are forced to question what, if anything, we can infer about sensation from spike trains of sensory neurons. Nonetheless, there is a phenomenon that incorporates sensation, namely consciousness itself, which could conceivably be "emergent," a second-order cybernetics concept.

2. Shannon's "general communication system"

Figure 1 recapitulates Shannon's "general communication system" (Shannon, 1948). As Shannon explained, it involves "An *information source* which produces a message or sequence of messages to be communicated to the receiving terminal," "A *transmitter* which operates on the message in some way to produce a signal suitable for transmission over the channel," a *channel*, where "The *channel* is merely the medium used to transmit the signal from transmitter to receiver," a *receiver*, where "The *receiver* ordinarily performs the inverse operation of that done by the transmitter, reconstructing the message from the signal," and a *destination*, where "The *destination* is the person (or thing) for whom the message is intended" (Shannon, 1948, all original italics).

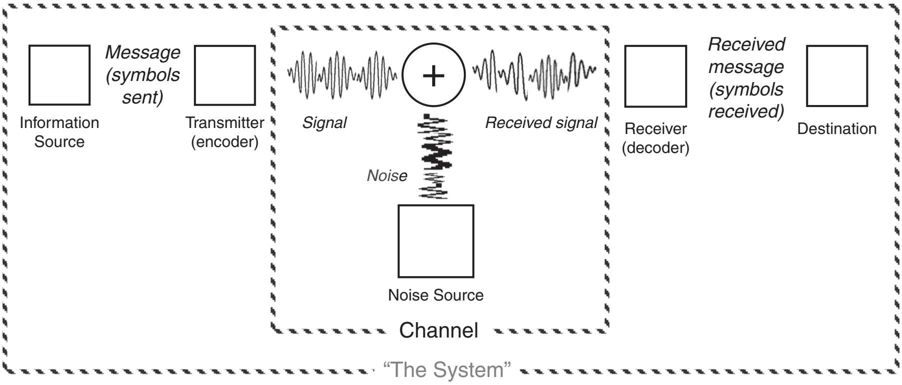


Figure 1.
The "general communication system" to which Shannon applied his information theory

Sent messages consist of symbols, for example letters arranged into words and then into sentences (Shannon, 1948). The symbols, and the meaningful groupings that they make, have different probabilities of being used, and hence of being sent. Knowing those probabilities is one requirement for computation of the information transmitted in a message (Shannon, 1948). Nizami (2010, 2011a, b, 2013, 2014a), among others, has summarized the relevant algebra.

In Shannon's system, signal distortion was imagined as caused by "noise" added to the transmitted signal within the channel. In reality, the conversion of messages to signals, and of received signals to received messages, is not distortion-free, and Shannon did admit that "at one of the terminals [sic], the signal may be perturbed by noise" (Shannon and Weaver, 1949, p. 34), although noise was still presumably added. In sensory systems, however, noise has been found to be multiplicative rather than additive (e.g. Lillywhite, 1981; Prucnal and Teich, 1982; Manahilov *et al.*, 2004; Klein, 2006; Wojtczak and Viemeister, 2008; for a list of other relevant papers, see Medina, 2011). Altogether, when all possible electrical sources of signal distortion are accounted for, Shannon's system is symmetric about an imaginary vertical axis in the middle of Figure 1. That is, Shannon's system's right-hand-side is physically a reflection of its left-hand-side. That symmetry will prove important to the following arguments.

Note that in cognitive science, the terms "symbols sent" and "symbols received" were sometimes replaced, respectively, by the terms "events" and "outcomes."

3. Why use Shannon Information Theory in neuroscience?

Applying a sensory stimulus to an organism such as a man or a Guinea pig, which has peripheral sensory organs, may evoke firing of voltage spikes in the neurons leading brain-wards. The applied stimulus itself might be changeable along a single continuum (i.e. a characteristic such as intensity), or might be changeable along many continua simultaneously, for example those that altogether result in a Gestalt such as a face. Regardless, any measure of the stimulus-evoked neuronal response (such as the number of voltage spikes, or the mean interval between them) will have a different value during (some given sub-interval of) each repetition of a stimulus. Over stimulus repetitions, then, the likelihood that the neuronal-response measure's value lies within any two limits can, for infinitely close limits, be approximated by a probability density function, having a mean value and a variance. The mean value systematically changes as the stimulus characteristic(s) likewise change. More than one (usually neighboring) neuron can be examined simultaneously (e.g. see Averbeck *et al.*, 2003); regardless, the conclusions reached presently apply equally well to one neuron, or to many.

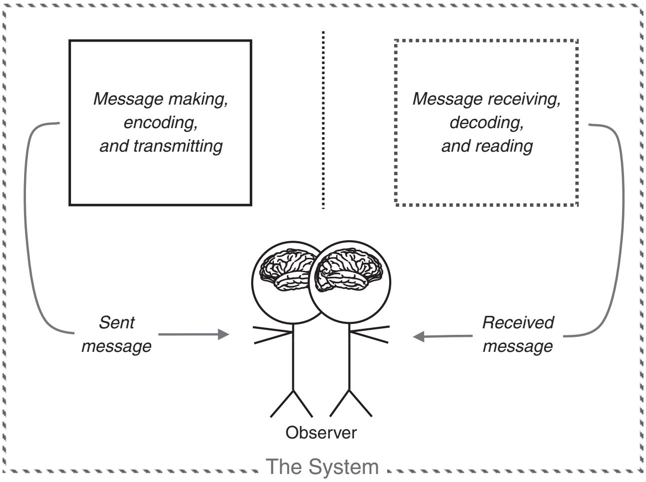
The inherent "confusion" of neuronal firing was taken by neuroscientists to reflect the noisiness of the Shannon channel (which is what Shannon's Information Transmitted effectively quantifies). If changing a characteristic of a stimulus (e.g. its intensity) caused a change (in the same direction) in the mean value of some statistically distributed feature of the spike-train, then the respective set of stimuli became Shannon "events" ("symbols sent") and the respective differing spike-train responses became "received signals."

4. Shannon's missing piece: the observer

Contrast the above concepts to that of Shannon's "general communication system" (Figure 1), in which the string of received symbols ("outcomes") is examined by a recipient at the destination. Who, to neuroscientists, is the recipient? This question proves crucial, as detailed below. Shannon Information Transmitted can only be computed by knowing the received symbols, and two other things, starting with what symbols were sent – known by the sender at the source, but not by the recipient. Not known, that is, unless the sender and recipient are the same person, the observer. If the observer also knows the probabilities of sending each different symbol, then the observer can compute the Information Transmitted.

Figure 2 shows the observer, in a version of Figure 1 which also emphasizes the aforementioned symmetry of Shannon's system.

Of neuroscience papers that present "information transmitted," few ever discuss the underlying concepts. Neuroscientists actually imagined themselves as sampling a system, the experimenter being part of the "environment of the system" (Walter and Gardiner, 1970, p. 344), not part of the system itself. Figure 3 illustrates this notion. The



Notes: The arrow pointing towards the observer from the left emphasize that, even when not being the sender, the observer knows what the message is

Figure 2. After Figure 1: the Shannon "general communication system," amended to show its symmetry and to include the observer (see text)

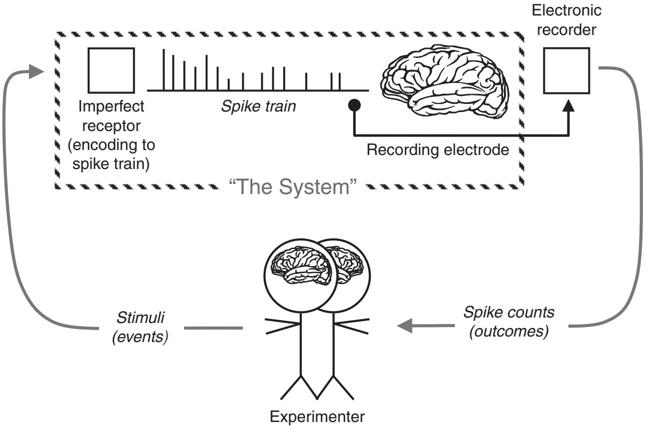


Figure 3. Shannon's "general communication system" (Figure 1) and its relationship to the experimenter (e.g. the neuroscientist), all as construed by neuroscientists (see text)

same is evident in *Spikes: Exploring the Neural Code* (Rieke *et al.*, 1997). *Spikes* is devoted to the application of "information theory" to sensory neuronal firing. Tellingly, the book lacks any illustration of its authors' operational interpretation of Shannon's "general communication system," containing only a copy of Shannon's original (and incomplete) box-and-line diagram.

Note in Figure 3 that Shannon's system's "reception" side (Figure 2: right-hand-side) is absent. That is, there is no conversion of "signal" back to "message" ("decoding") in the research animal's body. For "information transmitted" to have meaning, then, a substitute is required for the missing parts, and neuroscientists found one: Homunculus.

5. Ladies and gentlemen: Homunculus

Neuroscientists portrayed Homunculus as a miniature "being," a small copy of its host animal, living within each animal's head, but without the animal's awareness. Homunculus sees the neuronal voltage spikes, and hence infers the stimulus, although the literature does not describe how (more below). Figure 4 illustrates Homunculus' role. Hypothetically, Homunculus can (by unknown means) "decode" the spike train and thus infer the stimulus. Homunculus might even, if having a brain, "remember" the spike trains evoked over repeated presentations of the stimulus, in order to associate one with the other and hence possibly improve discriminability. But can Homunculus therefore quantify discriminability by computing "information transmitted"? No, not without knowing the probabilities of the stimuli, which are decided by the experimenter and which Homunculus, if trapped within the animal, cannot know.

Note that Homunculus needs legs (or their equivalents) in order to roam the brain; arms, in order to isolate particular neurons; and eyes, with which to observe spike firing. To coordinate these capabilities – and possibly to remember the observations, in order to better "discriminate" between stimuli in the future – Homunculus needs a brain. But that brain needs a sub-Homunculus within it, to perform computations on

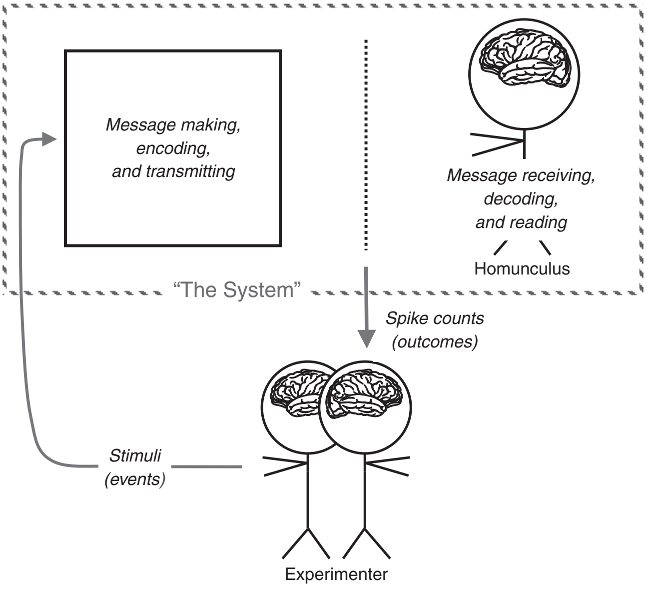


Figure 4.
Homunculus and its role, according to neuroscientists (see text)

behalf of Homunculus – and so on and so forth, to an infinity of Homunculi. An infinity of Homunculi is absurd. Further, inferring any stimulus might require infinities of time and/or energy. To unquestionably avoid infinities requires avoiding sub-Homunculi – leaving a single super-human Homunculus, the obvious candidate being a man-made invention called God.

But superstitions are unacceptable. Who plays Homunculus, then? The obvious candidate is the experimenter. But the experimenter does not know "the neural code," and therefore cannot "decode" the spike train; the experimenter can only make inferences (Nizami, 2014a). Figure 5 shows that no-one, therefore, takes Homunculus' place. Neuroscientists' "information transmitted" hence indicates, at best, how well neuroscientists can (on average) discriminate among the presented stimuli, through the research animal's neuronal firing.

Unfortunately, neuroscientists seem to see nothing of this.

6. Homunculus in the popular book *Spikes: Exploring the Neural Code*

Few writings on the use of Information Theory in neuroscience discuss its conceptual basis. One of the few that does is the book *Spikes* (Rieke *et al.*, 1997), which (according to GoogleScholar) has been cited 2,500 times to-date. The prefatory remarks therein, along with the first chapter, lay the groundwork for a subsequent plethora of equations and computations. Homunculus appears early on. On page xvii of *Spikes*, the page preceding the first chapter, Rieke *et al.* (1997) introduce the "disquieting figure of a little hobgoblin sitting up aloft in the cerebral hemisphere." Rieke *et al.* (1997, p. 1) then leave the brain and return to the laboratory, noting that there can be "an observer outside the cell" who sees "the electrical signals from individual cells [i.e. neurons]." Rieke *et al.* (1997) swiftly return to the inner observer, "a little man […] who observes the responses of his own sensory neurons and finally forms the percepts that the organism experiences" (p. 13). Rieke *et al.* (1997) then seem to unify the observer-in-the-lab with

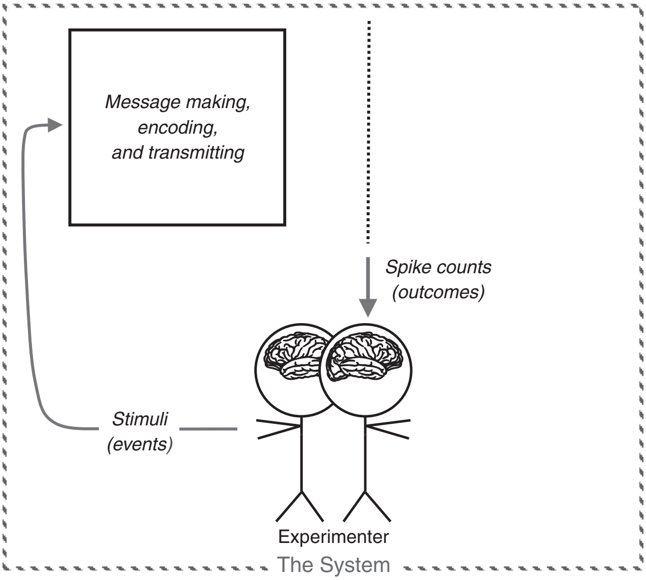


Figure 5. The actual system of a sensory neuroscience experiment (see text, and compare to Figures 2 and 4)

the observer-in-the-brain: “we place ourselves, inevitably, in the position of the homunculus – we observe the responses of sensory neurons and try to decide what these responses could mean to the organism” (p. 13). Rieke *et al.* (1997) are now a single thought away from proposing that Homunculus and the experimenter are one and the same. Then, remarkably, they change their minds (p. 14):

> It is easy to imagine that the task of the homunculus is trivial – after all, he just watches a projected image of the world as it flashes through the brain. But this projected image is *encoded* in the patterns of action potentials generated by the sensory neurons. It is not at all clear what the homunculus would have to do, even in principle, to make sense out of these encoded data. We propose that “understanding the neural code” means that we would know how to make sense out of the bewildering array of spike trains streaming in from the sense organs: If we understand the code, we can function as the homunculus [*sic*].

Notwithstanding the apparently unselfconscious expression “make sense,” Rieke *et al.* (1997, p. 14) have placed Homunculus (at least momentarily) within the brain, tasking the neuroscientists with “seeing” whatever Homunculus “sees.” Rieke *et al.* then mention Green and Swets (1966/1988), and the latter’s two-alternative psychophysical discrimination experiments (leading to d'), which call for Homunculus to function in “a world of two alternatives” (Rieke *et al.*, 1997, p. 15). Rieke *et al.* duly note the contrived simplicity of such experiments. Rieke *et al.* then return to the natural world, in which the animal does not follow the laboratory procedure (used to build d', for example) of averaging “signals” over relatively long time periods. Rather, the animal has a Homunculus who must “give a sort of running commentary or simultaneous translation” (Rieke *et al.*, 1997, p. 15) of the animal’s surroundings. Once again, the brain is the seat of Homunculus. Nonetheless, Rieke *et al.* (1997) then declare that “the statistically sophisticated homunculus would report confidence levels on his estimates of what is happening in the world” (p. 16), a task which, requiring statistical tools, would make Homunculus the equivalent of a laboratory personage equipped with textbooks and software and computers. Rieke *et al.* (1997) subsequently explain that “We [i.e. the experimenters] place ourselves in the position of the homunculus, monitoring the spike trains of sensory neurons” (p. 16). Once again, Homunculus is the equivalent of a laboratory personage. But there is more than one Homunculus now: “Out of many possible homunculi, there is one that tells us as much as possible about the world given the noise in the spike train data itself” (Rieke *et al.* 1997, p. 16). But which one? Only one can be dealt with: “Most of this book is about the problem of an impoverished homunculus who looks at the spike train of just one neuron at a time” (Rieke *et al.* 1997, p. 16). Is this particular Homunculus now the experimenter?

Rieke *et al.* (1997) confuse things further: they declare that “decoding” is “the problem solved by our homunculus” (p. 17). Rieke *et al.* fail to explain why a Homunculus at the brain would have to “decode” anything, given that spike trains provide the impressions of the world. Only an out-of-body laboratory Homunculus would conceivably need to “decode” spike trains – that is, in order to experience sensation as a research animal does.

Among the few neuroscience publications which do discuss the conceptual basis of their use of Information Theory is Walter and Gardiner (1970). They rejected Homunculus outright: “It may be thought that the parts of the brain whose function we have been formulating are merely subservient to some higher center, perhaps inhabited by a ‘little green man’, who really runs that brain […] [but] we have not found the concept of a higher and qualitatively different type of brain function to be a necessary hypothesis” (Walter and Gardiner, 1970, p. 371).

7. On the infinite regression of Homunculi

The present author uncovered the concept of an infinite regression of Homunculi within the human mind following upon his discovery of a hidden infinite regression of Homunculi within putative sensory receptors (Nizami, 2009a) in an erroneous multi-paper model of perception authored by K.H. Norwich (scrutinized in Nizami, 2009b, 2011b; and elsewhere). After the present author completed the first draft of the present manuscript, he discovered the literature on Consciousness, which provides a variety of relevant papers. For example, Kenny (1971), among others, notes that the infinite regression was recognized centuries ago. That is, René Descartes, quoted in Kenny (1971, p. 66), warned against the internal Homunculus who "sees" images for us within the brain (a phenomenon now called the "Cartesian theatre"). Kenny (1971, p. 68) notes a passage from vision scientist R.L. Gregory from 1966 that also warns against the use of the Homunculus in vision – while, remarkably, inherently assuming the Homunculus! Altogether, Kenny (1971) demonstrates that the infinite regression is difficult to avoid. This proves prophetic, as follows.

Attneave (1961) seeks to dismiss the problem of an infinite regression of homunculi. He declares that "If a homunculus exists it must certainly be composed of neurons" (p. 778). Then, "We fall into a regress *only* if we try to make the homunculus do everything" (Attneave, 1961, p. 778; original italics). Further, "The moment we specify certain processes that occur *outside* the homunculus, we are merely classifying or partitioning psychoneural functions; the classification may be crude, but it is not in itself regressive" (Attneave, 1961, p. 778, original italics). Attneave (1961, p. 778) continues: "Indeed, one might even hypothesize a series of concentric or nested homunculi without falling into a regress, provided each contained an outer layer of functions not contained in the next smaller one." To explicate a Homunculus, Attneave (1961) borrows from a contemporaneous paper (in the same volume) by Bullock; in Attneave's words (p. 778), "For any given behavior there must be at least one neuron that 'decides', on the basis of activity in receptors and other neurons, whether to initiate that behavior or not" (original internal quotation marks). Therefore "There may be as many 'homunculi' of this sort as there are coherent behavior patterns" (Attneave, 1961, p. 778; original internal quotation marks). That is, to Attneave, a Homunculus is a controller (a term used many times in the subsequent literature), one that can be physically outside of, but connecting with, the "behaviors" – that is, the "functions" – that it controls.

The Attneave (1961) model of the nested Homunculi is used by Dennett (1981) and by others (e.g. Crick and Koch, 2000, 2003). Attneave's (1961) claims beg a crucial question: how has Attneave managed a seemingly impossible task, namely, maintaining a finite number of Homunculi – while avoiding an infinite regression of Homunculi for one or more (potentially, each and every) Homunculus? Attneave's (1961) "nested" model is remarkably vague, consisting of the few sentences mentioned above. Perhaps it intentionally lacks detail. Attneave himself is no longer available to provide interpretation. In fact, Attneave's (1961) nesting scheme can be proven to be nonsense, but room is not available here. Essentially, Attneave "solves" the infinite regression by ignoring it. Dennett (1981) likewise imagines a committee of Homunculi who perform functions. Each Homunculus is allegedly composed of less intelligent Homunculi, all performing functions, until reaching a level at which each one "can be replaced by a machine." But this is just Attneave's model without the "non-controlled" functions; that is, it is Attneave's model with all functions being Homunculus-controlled.

The model of Attneave (1961) and Dennett (1981) seems unconvincing. However, there is a possible Cybernetics approach to the removal of Homunculi, namely, a general-systems-theory approach, such as emergence, which closely relates to self-organization (see e.g. chapters 6, 23, and 24 of Ramage and Shipp, 2009). For example, to von der Malsburg (1997), eliminating the Homunculus is inseparable from explaining Consciousness, but "Consciousness doesn't reside in any specialized faculty of mind or localized structure of the brain, but is rather a cooperative phenomenon of the whole brain or mind" (p. 203). To make his point, von der Malsburg (1997, p. 203) quotes John (1976, p. 1): "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" (original italics, and original internal quotation marks).

8. Final discussion and conclusions

Shannon (1948) provided equations quantifying Information Transmitted for a physical model which he called a "general communication system." Psychologists (starting with Garner and Hake, 1951) and neuroscientists (starting with Werner and Mountcastle, 1965) independently re-labeled Shannon's system and assumed that their consequent "information transmitted" computations were valid information measures for entire individuals or for individual neurons, respectively (see Nizami, 2010, 2011a, b, 2013, 2014a). They were not (same citations). In particular, neuroscientists believed that Shannon's Information Transmitted measured how well neurons "discriminate" among stimuli. But no neuronal system is a Shannon "general communication system"; Shannon (1948) himself misled-the-way by labeling as "general" a system that was specific to telecommunications.

Shannon's system has a "reception" (decoding) side which physically mirrors its "transmission" (encoding) side, but actual neurons lack the "reception" side. Neuroscientists nonetheless insisted that decoding must happen. Hence, they turned to Homunculus, an internal being who allegedly infers stimuli from neuronal firing. But Homunculus is physically impossible. Neuroscientists' "information transmitted" calculations (and others, such as Signal Detection Theory *d′*) have therefore, at best, revealed how well neuroscientists, not research animals, can (on average) discriminate among stimuli through the animal's neuronal firing. Importantly, the concept of Homunculus (used by Attneave, 1961; Dennett, 1981; and Rieke *et al.*, 1997, among many others) appears in "theories of consciousness," but is obviated if consciousness proves to be "emergent."

Neuroscientists' "information transmitted" computations are irrelevant to the animal's experience. This explains a hypothetically crippling aspect of single-neuron firing, namely, an "information transmitted" of less than 1 bit per stimulus, representing an inability to distinguish among merely two choices (e.g. light and dark). This absurd result has arisen for vision (e.g. Optican and Richmond, 1987; McClurkin *et al.*, 1991; Tovee *et al.*, 1993; Gochin *et al.*, 1994; Heller *et al.*, 1995; Tovee and Rolls, 1995; Sugase *et al.*, 1999; Wiener *et al.*, 2001; Averbeck *et al.*, 2003, Figure 5; Osborne *et al.*, 2004, Figures 3, 7), for touch (e.g. Arabzadeh *et al.*, 2004, 2006; Saal *et al.*, 2009; Farfán *et al.*, 2011), for taste (e.g. Rolls *et al.*, 2010), for smell (e.g. Rolls *et al.*, 1996), and for hearing (e.g. Gehr *et al.*, 2000; Lu and Wang, 2004; Nelken *et al.*, 2005). Ironically, measures of "information transmitted" in peripheral neurons had once been distinctly larger (e.g. Werner and Mountcastle, 1965; Darian-Smith *et al.*, 1968; Kenton and Kruger, 1971; Smith *et al.*, 1983), quite close in fact to what had been found in psychology. All along, however, psychologists had inadvertently been measuring short-term memory capacity rather than measuring informational "channel capacity" (see Nizami, 2011a, 2013; confirming a six-decades-old suspicion of Miller, 1956). Memory is not a known property of peripheral sensory neurons; hence, the agreement between physiology and psychology was extraordinary. Or as Somjen (1972, p. 312) drily noted, "The possibility that this correspondence might be fortuitous cannot be dismissed without further study." In fact, fortuity had been assured by various means; Walter and Gardiner (1970, p. 364) noted, for example, that Werner and Mountcastle (1965) "chose the stimulus pattern with unusual care." Indeed, Werner and Mountcastle and their contemporaries listed above had jury-rigged the experiments (stimuli, recording conditions, choice of neuron and its adaptation state, etc.) to give the desired results (Nizami, 2014a).

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