Does Norwich's Entropy Theory of Perception avoid the use of mechanisms, as required of an information-theoretic model of auditory primary-afferent firing?

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Background: Norwich et al.'s Entropy Theory of Perception (1975-present) stipulates that (1) the auditory receptor is uncertain about the stimulus' intensity, (2) the uncertainty is the entropy H, calculated using Garner & Hake's classic interpretation of a model crucial to communications engineers, Shannon's Information Theory, and (3) for primary afferent neuronal firing-rate F, F=constant×H. H is available *any time* that the appropriate probabilities of occurrence of events and outcomes are known, because Information Theory ignores mechanisms. The Entropy Theory, being "information-theoretic", must likewise avoid mechanisms. Norwich et al. claim to comply, but do they? *Analysis/results:* All of the Entropy Theory publications, 32 years worth, were scrutinized. Norwich et al. stipulated throughout that a steady stimulus was a stationary stochastic sequence of microscopic sensory events, repeatedly *sampled* by the receptor, each sample returning a different stimulus intensity. But sampling is a mechanism, which the Entropy Theory cannot separate from sensory transduction, the event's "outcome" to Norwich et al.. Their attempted separation of events from outcomes produced inconsistent identification of "events", a non-problem in actual Information Theory, where each outcome is *defined* as one of the events. *Conclusions:* The Entropy Theory is not an information-theoretic model of primary-afferent firing.

1. Introduction

The Entropy Theory of Perception (1975-present) proffers a conceptual basis for all of sensation, and if true would have far-reaching consequences for neuroscience. In the theory, "multiple, parallel receptor-neuron units" *sans* collaterals [1,2] "carry essentially the same message to the brain" [3, p414; also 4,5], amplifying the single-unit response [1,3].

2. The Entropy Theory and Information Theory

The Entropy Theory is the "*informational* or *entropic* view of sensation" [4, p151; also 2, p355; 6, p936]. It prescribes neuronal firing rates based on the Garner and Hake [7] interpretation of Shannon's [8] Information Theory [1,4,6,9,10,11,12,13]. Figure 1 shows Shannon's "general communication system". Shannon [8] dealt with "events" and "outcomes", which he defined in context, as follows. *n* events are possible. It is not known which event is about to occur. What *is* known is an event's probability of occurrence p_i, i=1,..., n. The event that occurs is the outcome. Figure 2 illustrates these concepts.

If there is more than one event, then there is uncertainty about the outcome. Shannon proposed that uncertainty must obey three rules: (1) uncertainty must be a continuous function of the p_i; (2) if $p_i = 1/n$, that is, if all events are equiprobable, then uncertainty must increase monotonically with *n*; and (3) uncertainty must be the same whether computed as if the outcome occurred through a single step (choice), or through two successive steps. Shannon proved that the requisite [amount of] "uncertainty", "choice", or "information", called I_S, is

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

I_S is the source (signal) uncertainty, or "source information". Shannon noted that K "merely amounts to a choice of a unit of measure", so he set K =1. When the events are symbols "k",

$$I_S = -\sum_{k} p(k) \log p(k) .$$ (2)

Norwich [10, p82] explained his choice of model: "Information theory, because of its special structure which gives information as a function of the probabilities of a set of possible outcomes, is ideally suited to describe the perceptual process". Figure 3 shows the Entropy Theory interpretation of the Shannon general communication system. Channels transmit with errors; a digit (say) will not always be received as it was transmitted. For simplicity Norwich et al. assumed that the number of symbols sent and received are the same. The probability of transmission of symbol k given reception of symbol j is denoted $p_j(k)$ [14]. Then

$$\textit{information transmitted } I_t = I_S - E_S$$

$$= -\sum_{k} p(k) \log p(k) + \sum_{j} \sum_{k} p_j(k) \log p_j(k)$$ (3)

where

$$E_S = -\sum_{j} \sum_{k} p_j(k) \log p_j(k)$$ (4)

is the stimulus equivocation/uncertainty/entropy, here called H. When what is transmitted is identically received, $I_t = I_S$, the ideal "channel capacity" below which actual capacities lie. H was conjoined to neuronal firing by the "fundamental assumption of the entropy theory of sensation" [15, p86], that is, "In the case of the isolated receptor with its sensory neuron, H is directly proportional to the frequency of impulses in the neuron" [16, p187; also 1,3,5,10,11,17,18,19,20,21,22].

3. Information and the physiological receptor

In theory, H is computed by the receptor itself, as follows. "We can envisage a steady sensory stimulus as a stationary stochastic sequence of microscopic sensory events" [23, p164]. The events were different stimulus *intensities* which, to make the mathematics tractable, were replaced by an intensity continuum characterized by a probability density function [1,3].

A general communication system (after Shannon, 1948)

Imperfect (i.e. noisy) channel

Information Source

Transmitter

Message

Signal (event)

+

Received signal (outcome)

Noise

Noise Source

Receiver

Received Message

Destination

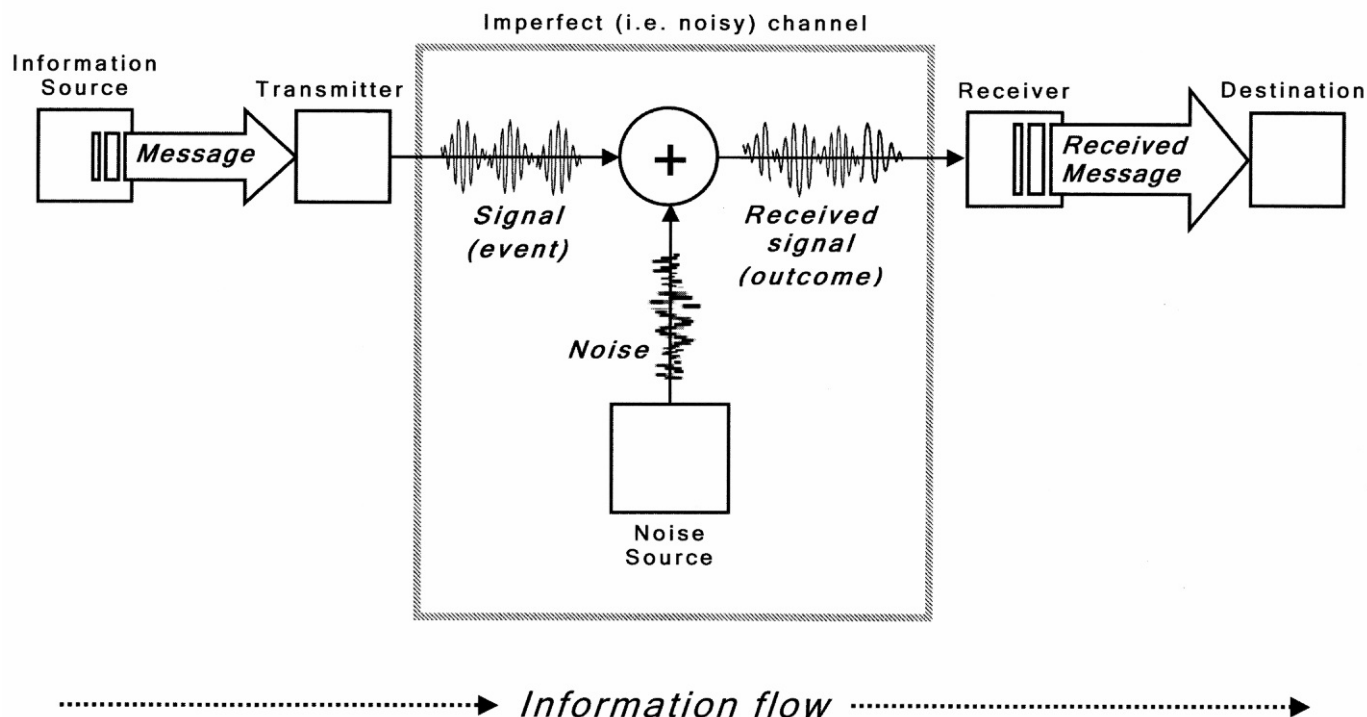············► *Information flow* ············►

Figure 1. A general communication system (after [8]), to which Shannon applied his Information Theory. Quoting from Shannon, the system comprises (1) "An *information source* which produces a message or sequence of messages to be communicated to the receiving terminal", (2) "A *transmitter* which operates on the message in some way to produce a signal suitable for transmission over the channel, (3) "The *channel* is merely the medium used to transmit the signal from transmitter to receiver", (4) "The *receiver* ordinarily performs the inverse operation of that done by the transmitter, reconstructing the message from the signal", and finally (5) "The *destination* is the person (or thing) for whom the message is intended".

Norwich [1, p288] explained that "by assumption, the microscopically structured receptor is concerned with reporting the mean stimulus intensity as inferred from a sequence of fluctuating microscopical samples. Receptor uncertainty at this most elemental level, then, can be taken to mean uncertainty about the mean intensity of a steady stimulus as inferred from individual samples of the stimulus" (see also [3,23,24]). That is, "The basic premise for calculating H is to assume that the receptor samples the sensory signal [the stimulus] to estimate the magnitude of the input [the stimulus intensity]. The uncertainty in signal magnitude is attributed to the variability or fluctuation in the signal at the receptor level" [22, page ICAD02-2; bracketed terms supplied]. Figure 4 illustrates these concepts. Norwich & Sagi [25, p807] named the auditory receptors as "the inner hair cells on the basilar membrane within the cochlea", and stated that "sampling" was needed for "the extraction of loudness information from the stimulus signal" [25, p810].

In the Entropy Theory, primary afferent firing does not encode a stimulus attribute (i.e. intensity), but rather, the receptor's uncertainty about the attribute [5,17,24]. From the Entropy Theory's conception to the present, its authors maintained that *"This is not a mechanism for a sensory receptor, but rather a principle following which the receptor may have evolved"* [17, p461; italics supplied].

To summarize: as the stimulus remains macroscopically constant, samples of its nature are continually available and allow a reduction of the receptor's uncertainty, H. On that uncertainty depend neuronal firing rates and loudness.

4. The lack of mechanism in Information Theory

Information Theory describes information transmitted after-the-fact, and with foreknowledge of all relevant probabilities of occurrences. As Theunissen & Miller [26] emphasized, Information Theory prescribes a *statistic*. A statistic is independent of mechanisms. That is, Information Theory does not and cannot specify what phenomena might produce, or be, "events" and therefore "outcomes". It cannot prescribe probabilities of occurrence. Thus, the computation of Information Theory quantities does not, need not, and cannot involve physical mechanisms. Remarkably, Norwich seemed to recognize this at one point: using the notation $J = H$ [11, p15], he stated that "The calculated information capacity, both in sensory science and in communications science, was *extrinsic* to the physical operation of the channel. By "extrinsic" I mean that the measure, J, of this information capacity never entered explicitly into an equation governing

the physical/physiological operation of the channel. For example, in the communications channel, the equations governing the operation of the electrical circuits which comprised the channel never contained the information, *J*, as a variable" [11, p17]. We may substitute "neurons" for electrical circuits; the point remains true
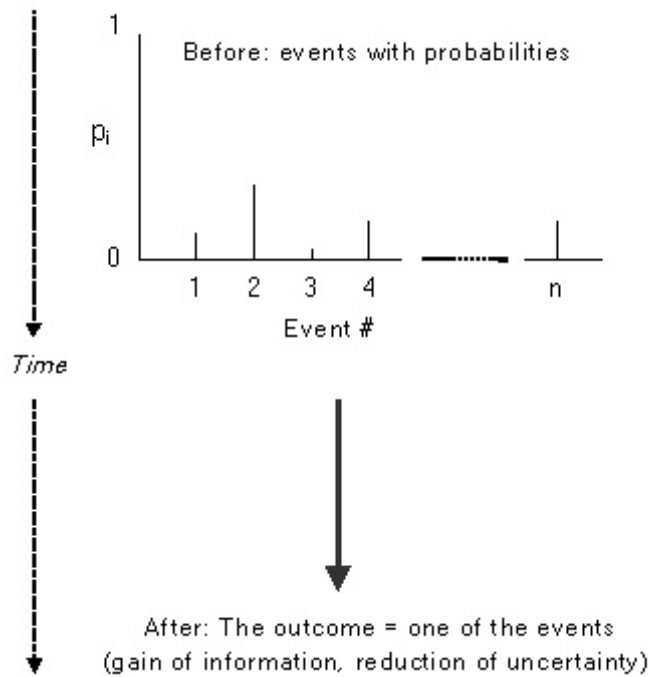

Figure 2. Events and outcomes. Events have probabilities. Each outcome is one of the events. Every time that there is an outcome, there is a gain in information (reduction in uncertainty).

5. Does the Entropy Theory avoid sensory mechanisms?

5.1 What the Entropy Theory says about mechanisms

Does the Entropy Theory actually avoid sensory mechanisms? Consider Norwich [27, p274]: "The entropy approach to sensory perception does not provide a molecular mechanism for the transduction of sensory events ... The entropy approach is akin to a thermodynamic law: it places constraints upon the nature of events, but does not posit the physical form that these constraints may assume. For example, in applying the entropy equation to calculate the maximum information to [*sic*] a sensory receptor perceiving a steady stimulus, we made use of a conservation of information constraint for the receptor-stimulus system: maximum information transmissible to the receptor = total uncertainty (entropy) associated with fluctuations of the stimulus. No mechanism, just a constraint."

Norwich and co-authors continually maintained the "no mechanism" claim; the Entropy Theory equations were " 'information balance' laws (akin to conservation laws), and not laws describing the mechanisms of sensory receptors" [4, p156]. Thus, supposedly, "No statement about how the receptor functions (chemically, electronically) has been made" [4, p180]. McConville, Norwich, and Abel [28, p157] stated that "The entropy theory does not address the mechanism of neuronal transduction and conduction, but provides parametric understanding about the theoretical limitations of the transducing system". Norwich and Wong [5] stated that "Clearly, it [entropy] is not to be a model of the mechanism of action of the receptor because, for example, the mechanism of olfaction is very different from the mechanism of hearing". Talking in terms of channel capacity, Norwich and Wong [23, p168] stated that setting $H < 1.8$ natural units of information creates a "seminal" equation for H that "does not provide the mechanism of sensation, but only the constraints leading to the sensory laws".

5.2 What is a mechanism? Sampling vs. transduction

The words of Norwich et al. are extraordinary. How are the theoretical limitations of the transducing system to be realised independently of the receptor's physical transduction processes, such as the aforementioned different mechanisms of olfaction and hearing?
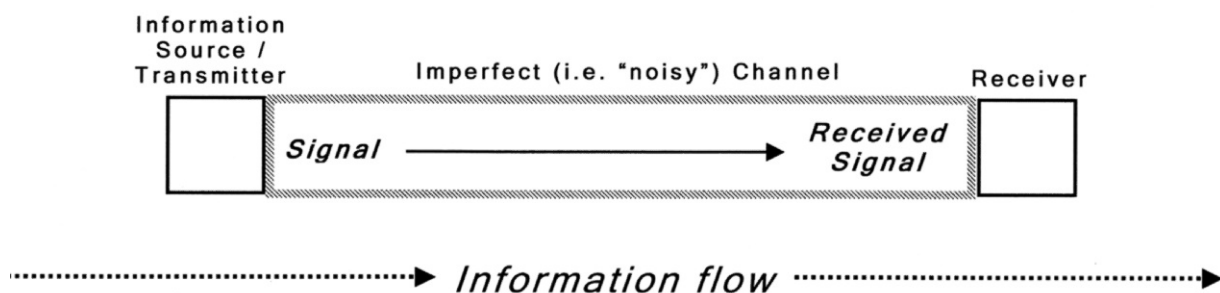

Figure 3. The Entropy Theory interpretation of Shannon's communication system. According to Norwich et al., "information" is "transmitted" from a "source" along a "channel" to a "receiver" [14,31].

Consider one definition of *mechanism* - "a machine-like device, system, process etc. by means of which some result is achieved" [29]. Sampling, in the context used by Norwich et al., must be a machine-like, repetitive process, involving physical interaction between stimulus and receptor, at the molecular scale. Such interaction is inseparable from transduction, "the way in which the electrical signal [in receptor cells] is generated by light or odor or sound" [30; bracketed terms supplied].

The Entropy Theory cannot separate sampling from transduction. This results in inconsistent descriptions of the sampled auditory "stimulus", whose allegedly fluctuating intensity was the Entropy Theory's "event". Once, the "stimulus" was a tone, made of a "spectrum of intensities" whose mean value remains constant [3]. Later, it was "the displacement of endolymph adjacent to a hair cell" [28]. Yet later, Norwich [31, p136] stated that "sound waves which activate the hearing mechanism consist of fluctuations in air pressure", an implied return to pressure as the sampled "fluctuating" stimulus. The "microscopically fluctuating stimulus" was not identified at all in the Entropy Theory paper of Wong and Figueiredo [22, page ICAD02-2], who declared only that "the auditory signal undergoes a number of transformations, from fluctuations in air pressure to fluctuations in fluid, before reaching the receptive sites. However, it is plausible to assume that signals of larger magnitude will be associated with greater fluctuations".

McConville et al. [28] represented the displacement variance, which they called the stimulus variance, by $\sigma_S{}^2$, and they represented the mean displacement by I, which they called the mean intensity of the stimulus. They then repeated a general relation between "stimulus variance" and "stimulus intensity" that has been a mainstay of the Entropy Theory since 1976 [32]:

$$\sigma_S^2 = \beta_1 I^n .\qquad (5)$$

The usefulness of this relation is cast in doubt by Norwich's own conclusions that "displacements of the basilar membrane in the cochlea are not related even in a linear manner to sound pressure levels at the eardrum (Rhode, 1971) [ref. 33 here]. Thus, the value of n "seen" or appreciated by the hair cell will differ from that obtained from the density of the air. Undoubtedly, fluctuations from other sources will also reach the hair cells" [1, p289]. Wong & Figueiredo [22, page ICAD02-2] changed the algebra slightly; they declared that "the monotonic relationship between variance and mean should take the form

$$\sigma_S^2 \propto (I + \delta I)^p$$

where I is the signal magnitude or mean, p is a constant that can be derived in principle from the physical considerations of the transduction process, and δI is a term that accounts for the non-zero fluctuations at the receptor level in the absence of a signal". Remarkably, Wong & Figueiredo made transduction central to the relation of stimulus fluctuation to stimulus mean, thus nullifying the idea that the Entropy Theory avoids mechanisms.
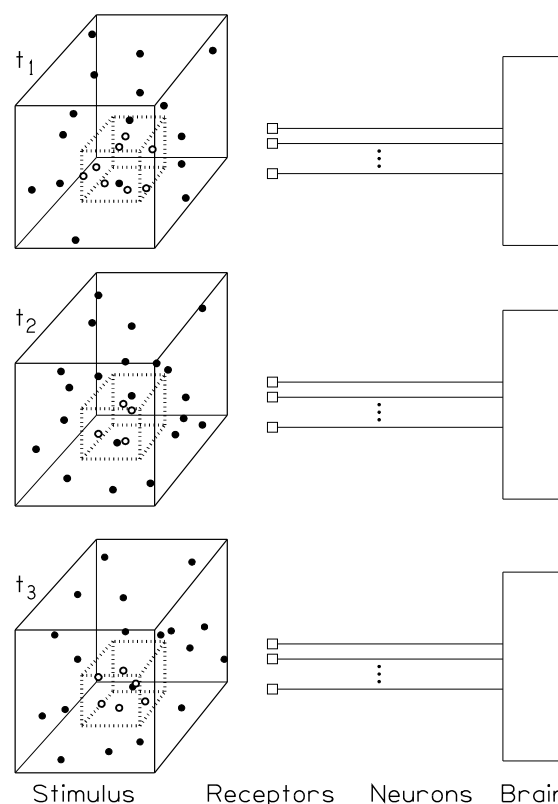
Figure 4. The Entropy Theory concept of the sensory response. This figure combines elements of Fig.3 of [3] and Fig. 2 of [1]. The stimulus was imagined as a gas or a liquid solution, that is macroscopically constant, here, by having the same number of particles (25) within the larger box. Within the smaller box, the number of particles fluctuates in thermodynamic equilibrium with the surrounding "reservoir" of particles. The number of particles within the smaller box varies from 8 at time t_1 to 4 at the later time t_2 to 6 at the yet later time t_3. At each of these instants, parallel, identical receptor-neuron units sample the contents of the smaller box without error, thus firing identically. Norwich et al. showed no equivalent illustration for hearing.

6. Summary and Conclusions

The Entropy Theory stipulates that Information Theory uncertainty is calculated at the receptor through sampling. Sampling is a mechanism, that must involve physical interaction of receptor and stimulus. But Information Theory does not and cannot specify mechanisms. Thus the Entropy Theory does not apply Information Theory appropriately.

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