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Comparing the Efficiency of Sensory Systems: A Biophysical Approach

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ABSTRACT. This article is an exposition of the view that the complexity of biological systems permits *intensive* (as opposed to *extensive*) research on any level. Specifically, (i) new views on *structural information theory* used to compare the efficiency of sensory systems in measuring the theoretically derived maximum amount of information in the sensory environment, (ii) the concept of the brain system involving the amygdaloid complex and the hypothalamus as a *coupled harmonic oscillator system*, and (iii) the concept of the cerebral cortex as an *e.m. interferometric (holographic) structure*, are outlined.

I. Introduction

Review of Philosophical Basis for Study of Complex Systems. If a research physiologist attempts to understand the reason for, and suitability of, a sensory system in any animal, he immediately comes up against the need for some criterion or measuring yardstick against which the sensory system can be matched. The biophysically oriented researcher is more likely to be motivated by such questions, rather than a desire for serendipitous discovery. The advocacy of a research plan or platform as opposed to research for discovery's sake has been made by Granit.¹ It shall be assumed here that understanding, rather than discovery of new facts, is the motive of the biophysically oriented researcher.

Given these motives, it follows that some form of abstract theory must guide research - in the case here considered: research in sensory physiology. Recently, Iberall² tabulated the types of scientific method: inductive, deductive, dialectic, mystical, pragmatic and abductive. Intended for the reader motivated by "why" type questions, this article advocates the mystical approach in which some central principle is taken as the unifying or explanatory principle behind many facts and systems. Lest the reader shy away from the word "mystical", I shall point out that the current beliefs in a natural world which is symmetrical, which can be described in a

mathematically elegant way and the engineering of which is the most *parsimonious*, are all mystical beliefs. This article on sensory systems is intended for the scientist who agrees that such beliefs or beliefs like them are at the core of his everyday research activities.

A distinction has been made between "intensive" and "extensive" research by Weisskopf.³ Intensive research is oriented toward the formation of fundamental laws, whereas extensive research is oriented toward the explanation of phenomena in terms of those fundamental laws. According to this view, the amount of intensive research being conducted at one time is always much less than the amount of extensive research. Anderson⁴ who opposes the view that only astrophysicists, elementary particle physicists, logicians and mathematicians and a few others conduct intensive research, has, on the other hand, pointed out that in the macrosystem the whole becomes not only more than but very different from the sum of its parts - a view which is neither atomistic nor holistic. Thus, symmetries and laws formulated at a very molecular level, i.e. the so-called fundamental laws, may be broken at a higher macroscopic level. Higher macroscopic laws have a property of "emerging" from the laws of a molecular level and surpassing them. From this viewpoint, relativity theory could be a "macroscopic theory" and Newtonian physics a "molecular theory". As one progresses from molecular events to macroevents, the amount of "broken symmetry" implies increased complexity and, according to Anderson, this increased complexity may be described by fundamental laws at any level, thus refuting the Weisskopf notion of intensive research as the calling of only a few.

In the same vein, one may claim that intensive research is conducted—must be conducted—in biophysics, because the complexity is ordered by its own fundamental laws. By an immersion in the known data, and with the desire to subsume a mass of observances under one or a few laws, one searches for a belief—a mystical belief—which will explain the all too many facts. We shall stress here this working method.

Turning now to the subject of empirical study of this article—sensory systems—one may hold, as a working hypothesis, to the simplification that nature consists of, in one sense, forms of information, and that the sensory systems of animals measure aspects of those forms. Now, a sensory system transmits or communicates information along pathways to higher order centers in the central nervous system. But such a transport function is much less important a problem than the one of procurement (of information). Having adopted a mystical belief in the form of nature dealt with by a sensory system—i.e., its informational aspect—one has a yardstick, or a ruler, with which one may gauge the ability of various designs of sensory systems to fulfill their purpose in measuring nature's informational structure.

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In the attempt to describe nature as an information structure, one has presently an intensive research problem.⁵ If the requirements of industry and society were extra-sophisticated in their need for information measuring devices, such a research orientation in this case would be merely extensive and not intensive. The ability of a biological sensory system to measure exceeds the ability of present day theory to describe what the system is measuring. In order to understand sensory measurement, the author has found it necessary to develop information theory a little, or, in other words, to engage in intensive research activities. We shall examine below three mystical beliefs which lead to testable hypotheses guiding research in sensory systems: (I) the belief that nature—in one sense—is an information structure and an animal's sensory system measures with varying degrees of accuracy that structure; (II) the belief that sensory systems of the "internal environment" of vertebrates, involved in the dynamic motivational processes of the brain, are part of a coupled harmonic oscillator system; (III) the belief that the registration of information from sensory systems is engineered in the most parsimonious way, i.e., elements of the cortex are multiply used by various informational inputs.

II. Information Structure

An interest in information structure leads one to the quantum analogy definition of what constitutes the smallest element having the ability to resolve uncertainty about a possible binary choice (A. Landé's original suggestion mentioned by Stewart,¹⁰ Koch,¹¹ Gabor,¹² Brillouin,¹³ Kharkevich,¹⁴ and Pimonow¹⁵). The early definition is that $\Delta f \Delta t = 1/2$, where Δf is signal bandwidth and Δt is signal duration, describes the necessary minimum element. Such an elementary signal was called a *logon* by Gabor.¹² However, such a definition permits the signal center frequency f_0 and center duration t_0 to vary. A later definition also requires a further informational quantum:⁶ $f_0 \cdot t_0 = 1/2$. A complete informational measure which is a Hilbert space representation is obtained for $\alpha\alpha^*$, where $\alpha = \Delta f \Delta t + j f_0 \cdot t_0$.¹⁶ The Hilbert space measure, $\alpha\alpha^*$, is a measure of energy distribution inhomogeneity and will indicate the number of degrees of freedom in the equations describing the system producing a signal as well as summed information measures.¹⁷ The Hilbert space measure will thus distinguish between the timbre of, say, a trumpet and a violin, as well as between a violin and a cello because the equations describing such systems differ in the number of degrees of freedom involved. More importantly for physiologists, such a measure ($\alpha\alpha^*$) should correlate with events at the basilar membrane.⁶ This measure is proposed in formulating a testable hypothesis about the basilar membrane.

This way of representing information observes the belief in symmetry and has certain practical applications. The following is an example. Corresponding to any number of characteristic functions describing a system, there are expressions $(\Delta f, \Delta t)_i$ and $(f_o, t_o)_i$, describing the distribution of energy (and thus information) in the system. Let us take four examples: (i) in which there is one characteristic function describing the system; (ii) in which there are two; (iii) in which there are three; (iv) in which there are n .

Thus, in case (i) we might have $(\Delta f, \Delta t)_1 = \Sigma_i (\Delta f, \Delta t)_i = 1/2$ for a minimum value. In case (ii) we might have $(\Delta f, \Delta t)_1 + (\Delta f, \Delta t)_2 = \Sigma_i \Delta f, \Delta t_i = 1/2$, for a minimum value; where $(\Delta f, \Delta t)_1 = 3/10$ and $(\Delta f, \Delta t)_2 = 2/10$; or $(\Delta f, \Delta t)_2 = 2/10$ and $(\Delta f, \Delta t)_1 = 3/10$; or any other combination, provided $\Sigma_i (\Delta f, \Delta t)_i = 1/2$. In case (iii) we might have $(\Delta f, \Delta t)_1 + (\Delta f, \Delta t)_2 + (\Delta f, \Delta t)_3 = \Sigma_i (\Delta f, \Delta t)_i = 1/2$, for a minimum value where $(\Delta f, \Delta t)_1 = 1/10$ and $(\Delta f, \Delta t)_2 = (\Delta f, \Delta t)_3 = 1/5$; or $(\Delta f, \Delta t)_2 = 1/10$ and $(\Delta f, \Delta t)_1 = (\Delta f, \Delta t)_3 = 1/5$; or $(\Delta f, \Delta t)_3 = 1/10$ and $(\Delta f, \Delta t)_1 = (\Delta f, \Delta t)_2 = 1/5$ or any combination, provided $\Sigma_i (\Delta f, \Delta t)_i = 1/2$. In case (iv) $(\Delta f, \Delta t)_1 + \dots + (\Delta f, \Delta t)_n = \Sigma_i (\Delta f, \Delta t)_i = 1/2$ with any combination of $(\Delta f, \Delta t)_i$ values. A similar treatment can apply to the relation f_o, t_o .

One can continue the explanation on into physiology:⁶ at the basilar membrane a traveling wave occurs with auditory stimulation which peaks at a place corresponding to the frequency of that stimulation. This peaking of the traveling wave is presumed to mechanically excite hair receptors. From our point of view, a Fourier transform is performed on the incoming signal. In cases (ii), (iii), and (iv) the center frequencies, f_o , of each $(\Delta f, \Delta t)_i$ may differ. Then different places on the basilar membrane are excited; yet when $\Sigma_i (\Delta f, \Delta t)_i = 1/2$, i.e., its minimum value, the information content would be similar, as the minimum value is equivalent to one bit of information.¹⁸ Even when not at its minimum value, as will be demonstrated below, the different dispersions of excitation would still be related to similar amounts of information.

The eigenvalues of the equation describing the system in which the energy of the signal was first stored or dispersed are correlated more accurately with the true situation at the basilar membrane. Suppose, for example, that $(\Delta f, \Delta t)_1 + j(f_o, t_o)_1 = (\Delta f, \Delta t)_2 + j(f_o, t_o)_2 = 1/2 + j1/2$ (i.e., $\Sigma_i (\Delta f, \Delta t)_i + j(f_o, t_o)_i = 1 + j1$); then $\alpha_1 \alpha_1^* = 1/2$ and $\alpha_2 \alpha_2^* = 1/2$ and $\Sigma_i \alpha_i \alpha_i^* = 1$. It could be that $f_{o1} = 4$ kHz; then $t_{o1} = 125 \mu s$, $\Delta f_1 = 1000$ cycles and $\Delta t_1 = 500 \mu s$; if $f_{o2} = 8$ kHz then $t_{o2} = 63 \mu s$, $\Delta f_2 = 2000$ cycles and $\Delta t_2 = 252 \mu s$. Now compare this case with $(\Delta f, \Delta t)_1 + j(f_o, t_o)_1 = 3/4 + j3/4$ and $(\Delta f, \Delta t)_2 + j(f_o, t_o)_2 = 1/4 + j1/4$ [i.e., $\Sigma_i (\Delta f, \Delta t)_i + j(f_o, t_o)_i = 1 + j1$ as before]. The situation is different, yet the number of logons is the same. But in the second instance $\Sigma_i \alpha_i \alpha_i^* = 5/4$, whereas this measure was 1 in the first instance. Similar demonstrations exist for differences between symmetric functions of differing degrees of freedom.

We see that the auditory system appears capable of measuring a quantum of information defined as $\Delta f \cdot \Delta t = 1/2$ and $f_o \cdot t_o = 1/2$. Now we ask of the less efficient systems. For example, suppose there are sensory systems which cannot measure to that fine grain of analysis; i.e., suppose $\Delta f \cdot \Delta t > 1/2$ and $f_o \cdot t_o > 1/2$ for some sensory system. What constitutes an informational quantum for such systems? In answering these questions, we may observe that the modulating envelope for the $\Delta f \cdot \Delta t = 1/2$ signal is a Gaussian shape and is the first of a series of confluent hypergeometric solutions to the Hamiltonian for a harmonic oscillator.⁵ The general solution for quantum information forms is: $\Delta f \cdot \Delta t = f_o \cdot t_o = 1/2(2n+1)$. Less efficient systems may measure solutions involving a higher order polynomial which would imply a fuzzy picture of nature. Some elementary signal forms are shown in figures 1-4 with the first modulating envelope shown giving $\Delta f \cdot \Delta t = f_o \cdot t_o = 1/2$.

As an example of a sensory system which measures only a fuzzy picture of nature, we may take the electric sense organ of the fish *Gnathonemus petersii*. The transmitter organ of this fish generates short pulses of about 200 μ sec duration of frequency range 1-10 kHz and at a rate varying between 0 and 5 pps.¹⁹ A voltage of about 6 volts p-p occurs between those points of the skin of the fish through which electric current flows. The field around the fish due to this electric current is similar to a dipole.¹⁹ The threshold field strength is roughly proportional to the distribution of *mormyromasts*, the supposed receiving organs of the fish. At the field's maximum, the electric field voltage intensity is 0.7 mV p-p/cm; the value of the threshold field voltage intensity when the fish is exposed to a homogeneous field parallel to its axis is about 0.2 mV p-p/cm. When no obstacle is in the environment of the fish, its transmitter produces a primary electric field strength of about 100 mV p-p/cm.¹⁹ Clearly, an elementary signal with modulation involving a Gaussian wave shape [i.e., $D_o(x)$ in figure 1] is not used in this case, as elementary signals above 3 kHz are 166 μ sec in duration or less [for $D_o(x)$ and $\Delta f \cdot \Delta t = f_o \cdot t_o = 1/2$] and far below the 200 μ sec observed by the fish in this frequency range. One must deduce, therefore, that the quantum of information for *Gnathonemus petersii* is either a signal with modulation involving polynomials higher than $D_o(x)$ —a Gaussian shape—or that the pulses emitted represent more than one quantum of the theoretically minimum kind. As no pulses of appreciably shorter duration were observed, one must conclude that elementary signals greater than those involving a $D_o(x)$ modulation are used by this fish.

Other investigations might involve the sense of touch. Oscillatory stimuli can be applied to the skin.²⁰ Therefore, definition of a tactile stimulus in terms of bandwidth and duration is also possible. An investigation could then proceed to empirically establish the minimum quantum for the sense of touch.

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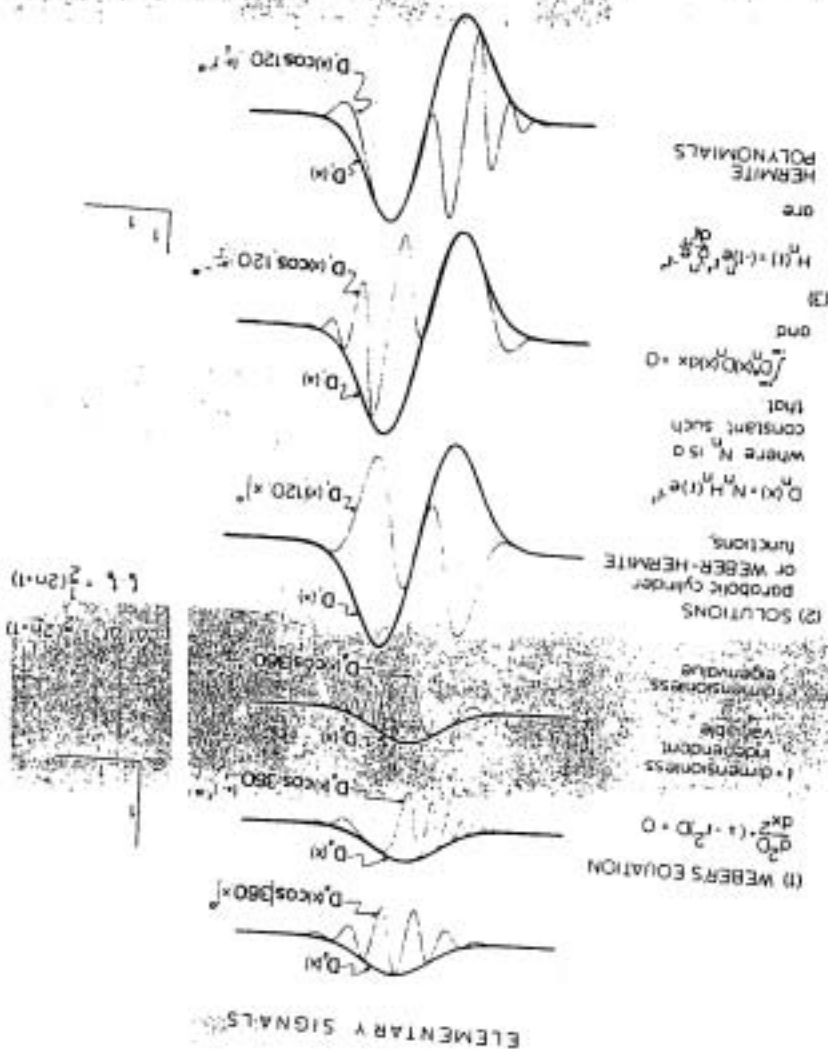
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Fig. 1. Elementary signals with amplitude modulations $D_1(x)$ and $D_2(x)$ in the first of each three, the modulated signal is a sinusoidal function in the second and third, descending. The frequency modulation is also frequency modulated, either ascending or change in frequency and f_0 is center frequency. Source for Figs. 1-4: Ref. 5.



ELEMENTARY SIGNALS

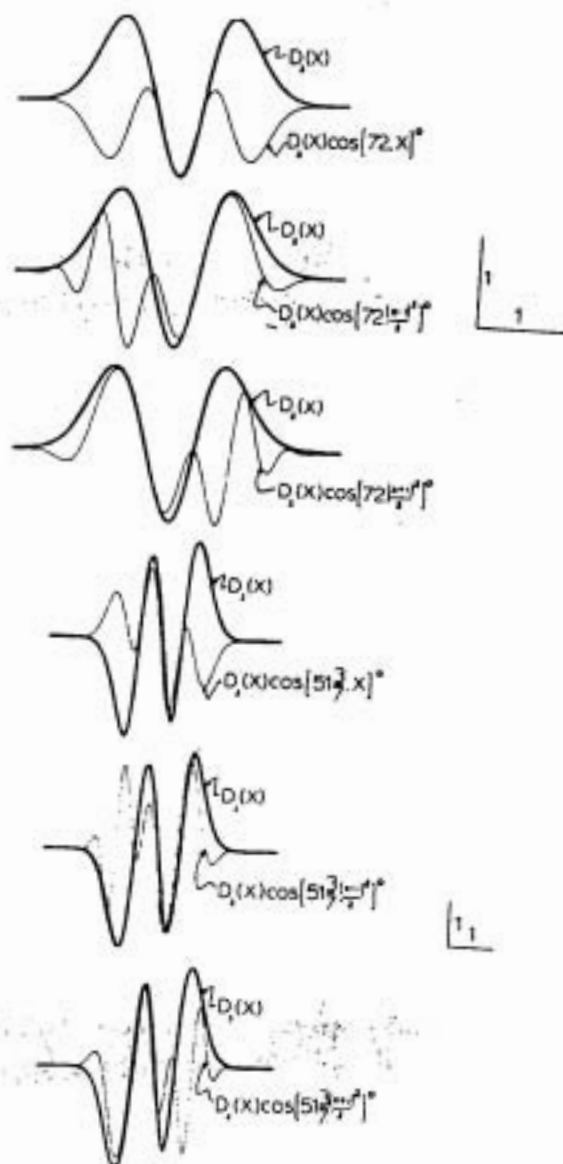


Fig. 2. Elementary signals with amplitude modulations $D_2(x)$ and $D_3(x)$, otherwise as in Fig. 1.

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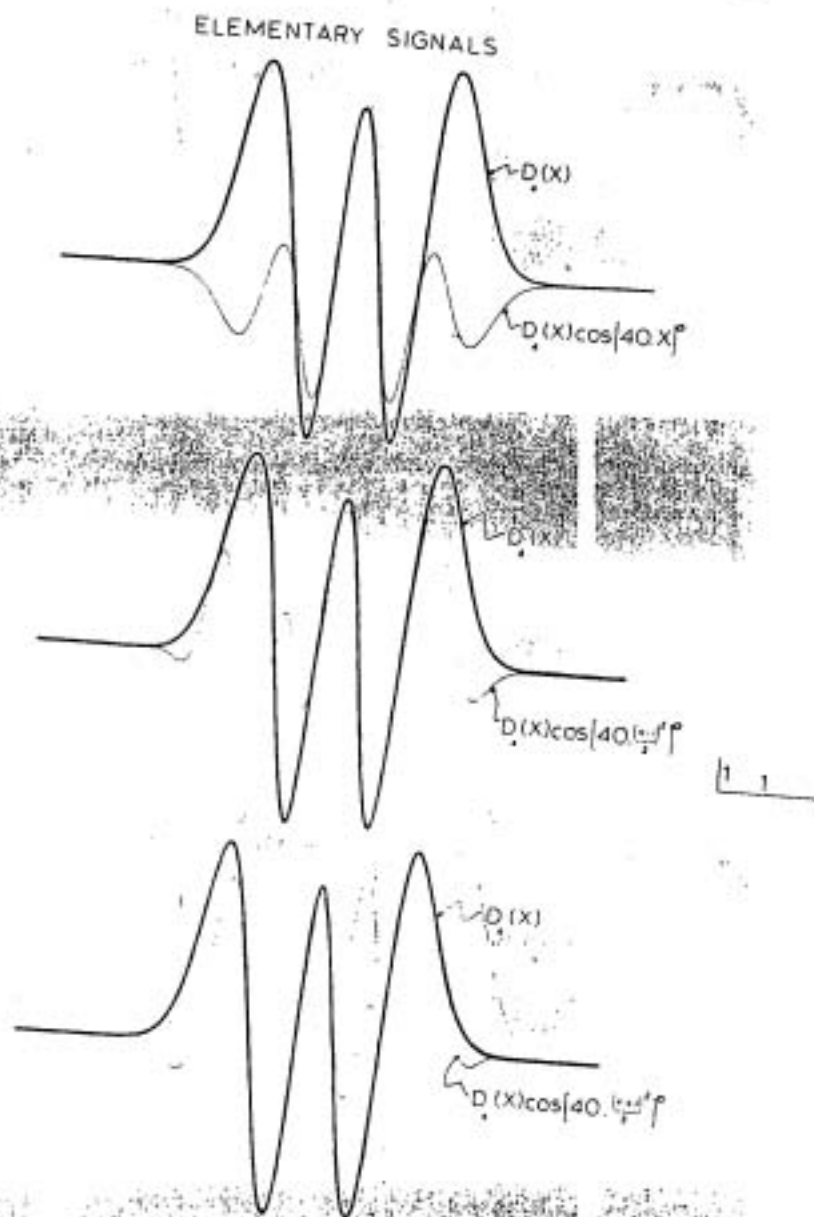


Fig. 3. Elementary signals with amplitude modulation $D_4(x)$, otherwise as in Fig. 1.

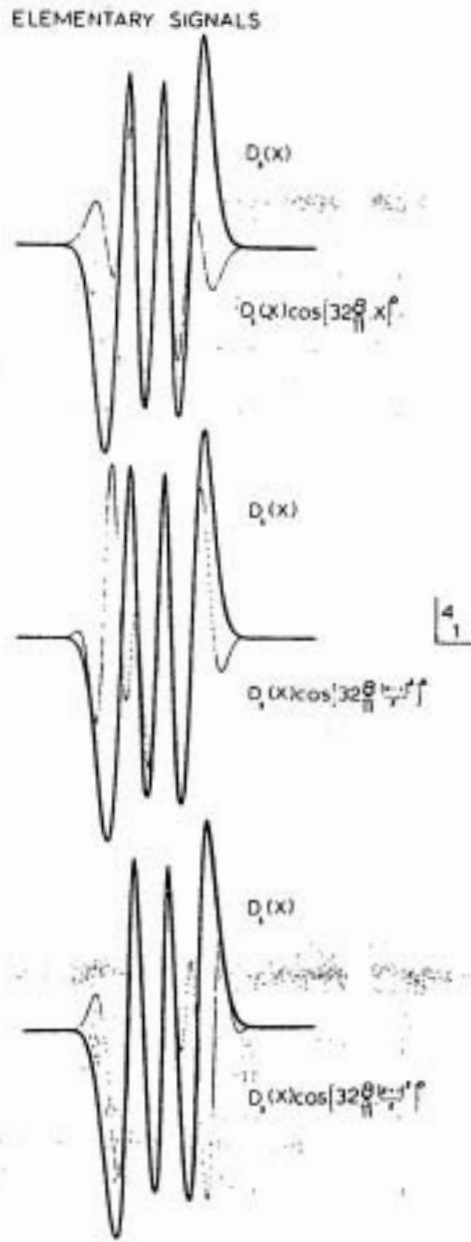


Fig. 4. Elementary signals with amplitude modulation $D_5(x)$, otherwise as in Fig. 1.

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Finally, the analysis presented here has applications to the investigation of information storage in the brain. In the case of the theoretically minimum quantum, i.e., $\Delta f \Delta t = f_0 \cdot t_0 = 1/2$, an electromagnetic field represents as much information as there are states of the field. Of course, biochemical events will influence the electromagnetic field, but the exchanges of brain and environment in terms of sensory messages and motor effectances are electromagnetic processes, i.e., the physiology or function is electromagnetic even if the structure is biochemical. The storage of information in electromagnetic terms becomes of central importance when the brain is considered.

Units of Measurement: I shall consider now the fundamental nature of the units used to describe signal dimensions. From our point of view, four signal dimensions are required to uniquely define an electromagnetic signal in informational terms.¹⁶ These four signal dimensions are: signal natural or midperiod (t_0), signal duration (Δt), signal average or midfrequency (f_0), and signal bandwidth (Δf). Their units are, respectively⁷: seconds/cycle, seconds, cycles/sec. or Hertz and cycles; t_0 and f_0 are defined over both the frequency (cycles/sec) and time (sec/cycle) domains and are reciprocal measures of a rate or succession and involve a *sequence* space in the terms of functional analysis. The quantities ' Δt ' and ' Δf ' which are defined over the "sec" and "cycle" domains, do *not* measure rate or succession and involve an *integration* space.

Bandwidth (cycle) has no real representation in the time (sec/cycle) domain—except by the bounding relations of an uncertainty product—and hence no real representation in the "second" domain. It is possible for a function to be defined in the "cycle" domain alone, and signal bandwidth is of this nature. Association with circular functions which do have both a frequency and time domain referent and representation has obscured the singular nature of signal bandwidth. The use of Fourier methods introduces a circular function redefinition and conceals the fact that prior to transformation no temporal referent existed. Of course, Fourier methods always presuppose infinite time¹²—and it is just this presupposition which should be questioned.

An example may be of use: a bandwidth of, say, 20 cycles is not a rate, i.e., the units used should not be Hertz; as the upper and lower bounds of the bandwidth may refer to 180-200 Hertz, or any other numbers with a difference of 20. It is, therefore, necessary to know the average or midfrequency (f_0) of the signal *before* the upper and lower bounds of the bandwidth (measured in Hertz) can be specified. According to this conception, bandwidth is only indirectly equal to the upper signal frequency passed minus the lower signal frequency passed. It is necessary to emphasize this observation lest the result of such a subtraction be erroneously conceived to be measured in Hertz. This would then be contrary to what is generally meant by bandwidth - as the term is not used to convey the idea of rate or speed. Thus, although bandwidth

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is not a rate measure, the signals passed through a bandwidth do have a rate - they are defined *both* in terms of cycles and seconds. It is, therefore, more than easy to fall into what I claim is an error of defining the bandwidth by the upper and lower frequencies passed.

Given that there are four (non-independent) dimensions to any electromagnetic signal, with two uncertainty relations relating these dimensions, the implication is that any electromagnetic field must be described similarly.

III. Coupled Harmonic Oscillators

To a certain extent, one may conceive the vertebrate nervous system as a third entity keeping equilibrium against disturbances from the first and second entities of the external and internal environments. The inputs from the external environment are *accepted* at a structure called the *hypothalamus* - an "internal environment sensory system".²¹ The problem, then, is to understand how these two separate inputs from the external and internal environments are reconciled within the third entity of the brain alone. The hypothalamus does not receive direct information from the external environment. However, it projects to and receives from the basolateral division of a structure called the amygdaloid complex, which does receive input a little more directly from sensory systems. The basolateral division of the amygdaloid complex is a multisensory system.²²

Thus, an input from the internal environment - such as blood sugar level falling - may result in an informational input from the *external* environment - such as the sight of food - being treated in a different way than if that particular informational input from the *internal* environment did not exist - i. e., the animal were not hungry. Allowing for discrepancies in timing of inputs from the external and internal environments - just after eating, blood sugar does not immediately rise to acceptable levels - the amygdaloid complex-hypothalamic system may be viewed as two coupled harmonic oscillators.²¹ The hypothalamic activities are periodic corresponding to the rise and fall of quantities in the internal environment conducive to the survival of the organism. The basolateral division of the amygdaloid complex is also in phase with this hypothalamic cyclic activity, thus - to take a specific example - placing "value" on the sight of food when the animal is hungry (and thus motivating the animal) and reducing this "value" when the animal is not. Indeed, one might say that the hypothalamus is concerned with the primary needs of the organism, and the amygdaloid complex with the secondary or derived needs or incentives.

After the amygdaloid complex is removed from an animal, the animal displays behavior which, among other aspects, indicates that incentives are "frozen" - food always tastes good no matter how much is eaten.²⁴ On the other hand, without an amygdaloid complex, the hypo-

thalamus cannot signal the needs of the internal environment. Thus, if the food is not visually present, an animal with no amygdala will tend not to engage in searching activity. It is a case of "out of sight, out of mind". Thus, if food is visually present, overeating occurs; and if food is available but not present to the senses, undereating occurs. This paradoxical behavior vis-a-vis the animal's physiological needs can be understood by the disjoin of the two coupled harmonic oscillators aforementioned.²⁴

IV. Holography Analogy

Brain research over the years has used some of the advances in models. At the turn of the century, when telephones were a novelty, the central nervous system was considered to function like a telephone switchboard. Now the brain appears to be much more elegantly engineered than any telephone system presently used. Recently, it has been established that the neural elements of the cerebral cortex are multiply used²⁵ and participate in the registration of many events, rather than being set aside for just one party line. The current widespread interest in holography or the registration of all the information contained by light waves on some kind of photographic storage material has inspired some writers, including the author, to adopt the mystical belief that the cortex of the brain functions in a way similar to a (temporal) hologram.²⁶⁻²⁹

The following argument may explain the author's adoption of this belief. Consider the most elegant, the most parsimonious engineering for a structure able to register informational events; then consider the positional registration that occurs when a solid structure - such as a pebble - disturbs in one place the surface of a yielding analog quantity - such as a pool of water. The local disturbance will - after some time lapse - be conveyed by waves to all parts of that analog quantity. The analogy is that positioning of the disturbance in a pool can be provided by anatomical specificity of connections to a cortical structure (i. e., cortical "wiring"). The cortex, as an analog "pool" of electromagnetic energy, has a determined input the place of which conveys specific information.³⁰⁻³¹ There are sufficient lateral interconnections in the brain as well as the possibility of electronic spread for the initial disturbance to spread to other areas.

A major problem in the analogy arises because there is no viewer of the electromagnetic pool who can judge that one disturbance occurred at time t_0 from a primary input, but that another disturbance - at the same spot - occurred at time $t_0 + t$ to an input at some distance from the point of observation because of lateral spread. To enable these events to be registered separately but without the need for a viewing homunculus, the belief can be entertained that the indigenous rhythms of the cortex provide a temporal gauge. I shall call this the problem of stimulus identification - with which, incidentally, the telephone switchboard belief was not plagued.

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Let us develop this viewpoint. Structures in the auditory pathway are arranged "tonotopically", i. e., for a particular frequency of the stimulus there is a particular place in a structure at which neurons fire maximally to stimuli at that frequency.³²⁻³⁴ On the other hand, nerve fibers are able to "follow" a frequency stimulus in phase by firing at rates commensurate with a direct neural representation of the stimulus in the time domain. This ability has been called "neural volleying", but does not seem to occur at frequencies above 4.5 kHz. Using the pool analogy, the tonotopic arrangement of the auditory pathway indicates that separate and distinct pebbles are thrown into the pool corresponding to the separate and distinct center frequencies of stimuli (f_o). Thus, a Fourier transform representation is obtained but only (i) of the frequencies (cycles/sec); (ii) on the cortical surface; and (iii) by neglecting temporal patterning.

The phase of the sensory signals can be coded in two possible ways. It is known that (i) neural volleying can represent the phase of signals below 4.5 kHz;³⁵ (ii) for signals at all frequencies a "coincidence detection" neural coupling might signal phase. Such a neural coupling has been demonstrated.³⁶ The latter occurs when the separate inputs of two neurons - the firing of which are out of phase and which lead to a third neuron - are arranged anatomically such that a discharge from the third neuron is only triggered when the two separate inputs are separated by a time interval (giving phase or absolute time differences independent of frequency). This delay can be arranged either by delay lines involving synaptic gaps which take time for an electrical charge to cross, or by slowness of passive electrotonic spread of the potentials in the third neuron elicited by the input from the first two neurons from different time sites, which ultimately trigger a discharge.

A possible way in which stimulus identification occurs would be if an inherent cortical rhythm were to be triggered by an input on its way to the cortex such that any succeeding stimulus would be affected by an excitability-inexcitability cycle. Such a rhythm has been demonstrated in the cat cortex to be of 100 msec duration.^{37,38} A pacesetting occurs in the moderately anesthetized cortex when gross evoked potentials are recorded - presumably occurring by passive volume conduction because no spike discharges from single cells are recordable in this state of anesthesia. Just how these passive potentials are related to the active electrogenesis of single cell spike potentials remains a mystery.

If stimuli are applied to the cortex of a moderately anesthetized cat cortex in pairs, one directly following the other, whether they be auditory, visual, somesthetic (i.e., concerned with the sense of touch) or even direct electrical stimulation, and cortical evoked macropotentials are recorded, the amplitude of these evoked responses differ. For example, with stimuli separation below about 100 msec, the second response amplitude is a fraction of the first; with stimuli separation approaching 100 msec, the second

response approaches the same height as the first, or there may even be an overshoot or heightening of the response amplitude to the second stimulus around 100 msec stimuli separation. These effects are, however, very much dependent upon the level of anesthesia. The percentage of the second response amplitude with respect to the first is known as the *recovery cycle*. In the moderately anesthetized animal the reticular formation of the brain - which is a kind of activating or amplifying system for the brain, among other things - is not active. The thalamic nuclei, through which sensory input must pass on route to the cortex, is active. Thus, it could be that here we have the trigger of the cortical pacemaker started in the thalamus by the sensory input on its way to the cortex. The result is a cortical rhythm which - because of the 100 msec periodicity of relative inexcitability - enables a temporal identification of incoming signals. Thus, the sensory input can be identified (after Fourier transformation) as occurring at a certain cortical position (with height of potential less than $S - s$). Also, the sensory input can be identified or uniquely registered as occurring at a certain cortical position after previous input to this position (with height of potential $S - T$, where T indicates the cortical inexcitability) or as occurring at another cortical position after a previous input at that position (with height of potential $s-t$). The temporal coherence of cortical excitability-inexcitability triggered by sensory input to the cortex thus provides a form of memory for identification purposes and for possible stimulus integration.

This cortical rhythm of 100 msec provides a temporal coherence and interferes with the incoming signal. As the rhythm involves analog waves and produces zero to 100% excitability within the 100 msec, informational coding ability of such a rhythm is not restricted to any limitations based on digital reasoning.

There appears to be a great deal of evidence that this neural mechanism exists.²⁷ The duration of 100 msec appears to be a critical period in mammalian cortical physiology. In electroencephalography (EEG) or the recording of massed potentials from the scalp, the alpha rhythm - which occurs when the subject's brain is relatively inactive - is 10 Hz, thus involving a period of 100 msec. Investigators studying the ability of the thalamic nuclei to "pace" the cortex in acute animal experiments have also noted to influence of this period. Cortical neurons are "paced" to fire at 100 msec intervals when thalamic neurons are electrically stimulated. Analog postsynaptic potentials in thalamic neurons also appear to last for 100 msec.

Other investigators³⁹ have recorded intracellularly (within the cell) from neurons in the diffuse thalamic nuclei during electrical stimulation of other regions of the diffuse thalamic system. Stimulation of one portion of the diffuse thalamic system produces heightened responses in other portions of the system. It has also been demonstrated that there are clusters of spikes (single cell firings) which occur at the end of each 100 msec inhibitory post-synaptic (analog) potential.³⁹

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These characteristic periods of the mammalian cortex thus may provide physiological evidence of an underlying structural connectivity. Areas of the brain other than the cortex may have their own particular rhythm. For example, the cat hippocampus has been demonstrated to have a characteristic slow (4 to 7 Hz) "theta" rhythm.

Possibly involved in this functional dependence of the cortex on thalamic triggering are those electrical phenomena known as *recruiting responses* and *augmenting responses*. Recruiting waves are surface negative at the cortical surface with long latency (ca. 15-30 msec) and with a smaller surface positive phase occasionally preceding and often following. Complex polyphasic forms are common. They are most easily elicited by stimulation of the medial one-third of the thalamus and occupy the upper dendritic layers of the cortex. They are maximally recorded in cortical regions other than the primary sensory projection areas with a distribution and morphology similar to that of spontaneous slow wave "recruiting spindles" seen in barbiturate narcosis and sleep.

Augmenting waves have a latency of approximately 10-20 msec, and follow the repetitively elicited primary sensory responses to stimulation of thalamic radiations at the same optimum frequency for recruiting responses. An augmenting wave is an increasingly large negative wave with a peak 5-15 msec later than the peak of the specific response negative wave.

Both recruiting and augmenting waves increase the amplitude of cortical responses to repetitive (5-10/sec) shocks to the thalamus. It has been demonstrated that even where the spontaneous rhythm of the cortex is low, weak shocks to the optic nerve are effective only when they fall in certain phase relationships with an inherent cortical rhythm which is not accompanied by a potential fluctuation in the record. An interval of about 0.2 sec or multiples of this can be found at which successive shocks will be equally effective. A slight change of phase relationships at the same frequency will alter the amplitude of the whole series of responses. A slight change of frequency will cause an alternating slow increase and decreases of successive responses in a manner strictly corresponding to beat frequency phenomena.

A single volley to the optic nerve synchronizes corticothalamic circuits even if they are asynchronous, and their summated responses then follow periodically as part of the cortical response to stimulation. the series of spikes which appear on the main cortical discharge may represent the repetitive discharge of cortical elements; when not appearing as separate spikes, temporal diffusion may fuse them to a smooth elevation. It appears that the sensory input alone requires to activate facilitatory pathways which enable the very same sensory input to be registered in higher order cortical centers.

However effective the first maximal shock to the optic nerve, the response to the second is maximal only after a 0.2 sec interval, being absent during an interval of 80-100 msec after the first. The cortex is thus accessible to a second stimulus only after the first stimulus has completed the circuit through the successive elements of the cortex. even with maximal stimuli, facilitation by corticofugal pathways is essential for passage of the critical synapses.

Thus, two coincidental inputs are required at the cortex to register a sensory input. One input is provided by the sensory input per se, and the other is provided by a thalamic volley which is triggered by the same sensory input. The cortex is therefore an interferometric structure.²⁸

Although precisely how information is registered in the cerebral cortex is an incomplete story, one may, at least, entertain the mystical belief that the cortex is some type of hologram and most assuredly is an interferometer. I stress the "entertain the belief" concerning whether the cortex is a hologram because, a priori, in certain cases the central nervous system does not record all the information in the physical signal.⁴⁰ It is ironic that information contained in light waves - for which the original holographic theory was designed - is incompletely registered in the visual system of mammals.²⁹

It is possible that pattern analysis in the visual system is achieved by mechanisms which behave like spatial filters. The spatial frequency of a grating is expressed as the number of complete cycles of dark-light bar pattern per degree of visual angle. It is not, therefore, a Fourier transform of light intensities. The visual system can behave like a spatial filter because it appears designed to be sensitive to contrast. The visual pathway, unlike the auditory pathway, is designed more for the registration of transients in stimulation than in the registration of the stimulation itself (although color vision is an exception to this statement). Thus, whereas structural information theory is based on the distribution forms of energy of an auditory stimulus, in vision a structural information theory might be based on the spatial - rather than temporal - distribution of light energy. Time in audition is not equivalent to wave frequency in vision, but spatial frequency. One may then question whether - corresponding to the $\Delta f \cdot \Delta t = f_o \cdot t_o = 1/2$ elementary quanta in audition - there are $\Delta f_s \cdot \Delta s = f_{o_s} \cdot s_o =$ a constant condition in vision (where Δf_s is spatial frequency bandwidth, Δs is extent of the signal, f_{o_s} is spatial midfrequency and s_o is midextent of the signal). The $\Delta f \cdot \Delta t = f_o \cdot t_o = 1/2$ auditory quanta refer to a constant signal wave energy distribution; the $\Delta f_s \cdot \Delta s = f_{o_s} \cdot s_o$ equals a constant spatial distribution of signal energy sources. In the case of vision, light is treated as either existing or not existing; but there is no treatment of temporal distribution. The analysis of visual stimuli in structural information terms also runs into complications due to the two dimensional nature of space as compared with

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the one dimensional nature of time. Furthermore, phase differences in spatial frequencies are not the same as phase differences recorded holographically. Indeed, spatial frequencies and spatial phase can be recorded by conventional photographic processes. A spatial phase is not, therefore, a direct stimulus of a three dimensional visual world at all.

I have touched on audition, vision and somesthesia as sensory systems amenable to an information theory analysis - with reservations about the visual sense due to the treatment of light waves as either present or absent and because the third dimension - phase - is not registered by the visual system (spatial phase having been discounted as having any relation to a visual third dimension). Elsewhere, I have called the visual world an incomplete transmitter of information.²⁹ We shall leave the chemical senses out of consideration here. This is because it seems likely at the present time that stimulation of chemical sense organs is based more on the structure of molecules than the chemical composition of the molecules themselves. One might almost believe that the structures being measured are actually used - maybe as an enzyme, maybe during a chemical reaction ionized radicals are exposed which affect the membrane structures. In any event, a structural information theory based on electromagnetic energy forms is not needed in describing the form of nature measured by the chemical senses; the structure is provided by molecular forms.

In summary, the complexity of biological systems permit intensive research on every level - not merely the molecular. In understanding and comparing sensory systems, a metaconception or mystical belief - *structural information theory* - has been adopted. The complexity of such systems has made the further development of structural information theory necessary. By using structural information theory as a metaconception of what is possible (for measurement) against which the efficiency of sensory systems to measure can be compared, a comparative analysis of sensory systems can be formulated. In understanding the function of sensory systems of the internal environment, a mystical belief - *coupled harmonic oscillators* - has been adopted. Finally, in understanding the information registration capability of cortical structures, a mystical belief - *electromagnetic interferometry* - has been adopted. It is suggested that the development of these beliefs is intensive research.

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