TWO CLASSES OF HOLOGRAPHIC PROCESSES
REALIZABLE IN THE NEURAL REALM

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Holography refers to a broad class of storage and retreival processes based on the recording of interference patterns. As a model for a neural memory system, holography provides both associative and redundant storage along with a mathematically explicit description of the system's operation. Lashley (1929) was among the first to propose that memory was coded in terms of neural interference patterns and was let to this conclusion by his discovery of redundant storage in the brain. Twenty-seven years later, Beurle (1956) showed how such interference patterns might be stored so that the original information could be retrieved without distortion. In 1963, van Heerden noted the similarity between Beurle's hypothesis and the more concise representation of the interference process offered by holographic theory. Subsequently, a number of authors have outlined, to varying degrees, the analogy between holographic and neural processes (Julesz and Pennington, 1965; Pribram, 1966, 1969, 1971; Westlake, 1967, 1968, 1970). Of these, only Westlake (1968, 1970) has given a detailed analysis of the neural mechanisms involved. His hypothesis, however, like Beurle's, places severe restrictions on the firing patterns of neurons that are at odds with the known properties of neural codes.

This paper will demonstrate that holographic storage can be obtained when only the most general neural codes are assumed. A recognition system employing transmission holography is proposed and the limited capacity of this type of storage for multiple recordings leads naturally to a modelling of short term memory. The system predicts a wide range of behavioral data in recognition tasks based on a single assumption concerning the properties of individual neurons.

Before detailing the neural holographic processes, a brief description of optical holography will demonstrate some of the properties of this method of storage.
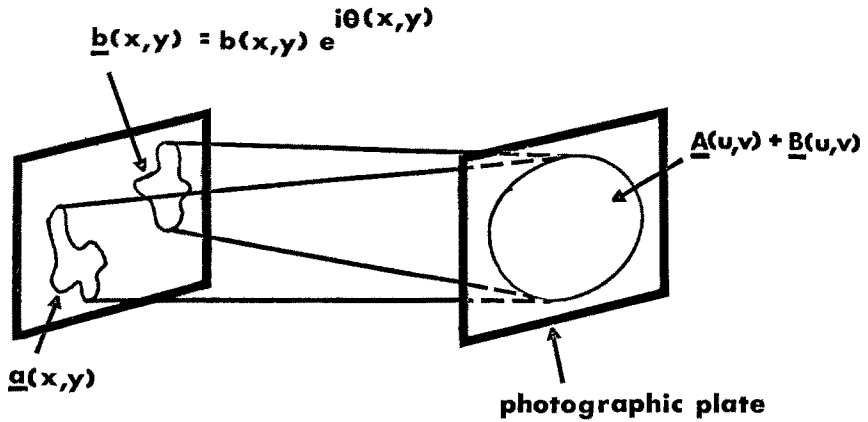
Optical Holography

Optical holography, developed by Gabor (1948), allows the recording of both the phase and amplitude of a wavefront of light. Since photographic plates are sensitive to intensity but not to phase, the plate is exposed to two wavefronts simultaneously and the resulting interference pattern is recorded. If both wavefronts are monochromatic and coherent in phase, a stable interaction occurs so that the interference pattern codes both amplitude and phase in terms of intensity variations. The recorded interference pattern is the hologram; illuminating the hologram with one of the original wavefronts causes the

reconstruction of the other. The hologram is thus an associative memory of the two wave-fronts.

If one of the original wavefronts was the light reflected from a three-dimensional object, for example, the reconstruction will be an exact replica of the object such that no visual test can differentiate the two. In other words, all of the phase and amplitude information has been recovered.

Figure 1 illustrates the two steps in the holographic process. $\underline{a}$ and $\underline{b}$ are wave-fronts that vary spatially in amplitude and phase, and $\underline{A}$ and $\underline{B}$ are their transforms at the photographic plate. The photographic plate is sensitive to recording energy, i.e. the product

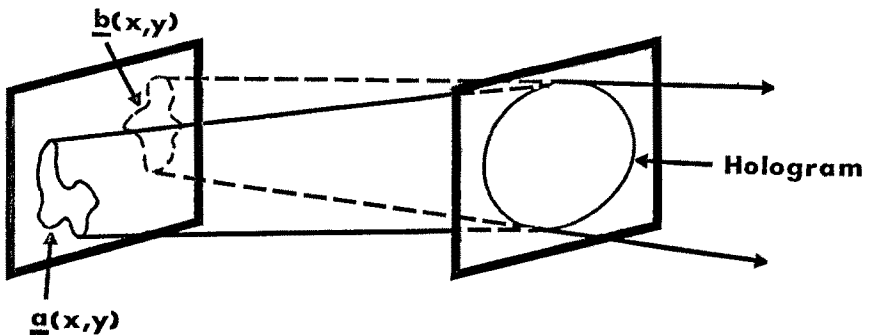**RECORDING**

RECONSTRUCTION

FIGURE 1: OPTICAL HOLOGRAPHY

of the recording intensity and the exposure duration.

$$E = t(\underline{A} + \underline{B})(\underline{A} + \underline{B})^{*} \tag{1}$$

$\underline{A}, \underline{B}$ - wavefront field vectors
E - exposure energy
t - exposure duration
$*$ - denotes complex conjugate

After developing, the transmission coefficient of the plate is a function of the exposure energy; if the function is linear, the resulting expression is

$$T = \beta E = \beta t(\left|\underline{A}\right|^{2} + \left|\underline{B}\right|^{2} + \underline{A}\underline{B}^{*} + \underline{A}^{*} + \underline{B}) \tag{2}$$

T - transmission coefficient
β - slope of transmission vs. exposure relation

If one of the original wavefronts $\underline{a}$, or more precisely, its transform in the hologram plane, $\underline{A}$, is incident on the hologram, the transmitted components are

$$\underline{A} \cdot T = \underline{A}\beta t(\left|\underline{A}\right|^{2} + \left|\underline{B}\right|^{2}) + \beta t \underline{A}\underline{A}\underline{B}^{*} + \beta t \left|\underline{A}\right|^{2}\underline{B} \tag{3}$$

The first term describes the transmission of the $\underline{a}$ wavefront at an attenuated amplitude; the second represents a complex wavefront dependent on both $\underline{a}$ and $\underline{b}$; the third is a complete reconstruction of the $\underline{b}$ wavefront attenuated by a real-valued variable that can be considered constant if $\underline{a}$ and $\underline{b}$ are independent.

Under appropriate recording geometries, the transmitted components propagate in different directions so that the reconstruction of $\underline{b}$ is available uncontaminated by the other wavefronts.

The hologram is an associative memory in that storage of $\underline{a}$ and $\underline{b}$ allows reconstruction of $\underline{b}$ upon reference by $\underline{a}$ and vice versa. It is a redundant or distributed memory (under certain transformation between the object field and the recording field) in that any part of the hologram can reconstruct the complete wavefront.

The essential requirement of the wavefronts that code object information is that they are monochromatic and phase coherent. These properties allow the wavefronts to interfere in a stable spatio-temporal pattern. In demonstrating the possibility of holographic storage in the neural realm, the first requirement is therefore to determine the locus of the stable interaction. Both Beurle (1956) and Westlake (1968) have assumed, as in the optical case, that wavefronts of neural spike trains are all of a single frequency and fixed in their relative phase. This assumption not only places unattainably stringent requirements on the stability of neural firing, but also is invalidated by the wide use of frequency in the brain for coding of stimulus attributes (e.g., intensity, cf. Perkel and Bullock, 1968).

Moreover, such an assumption is unnecessary in the discrete neural system as opposed to the continuous optical case; the structural coherence inherent in the fixed inter-neural connections of the brain already permit a stable spatial interaction of wavefronts regardless of the frequency and phase of individual spike trains. Since the interaction will however, very randomly in time (assuming random variation in interspike intervals), it must be shown that the mean spike rate is the dominant parameter in coding and storage. If this is the case, spatio-temporal stability is achieved and the maintenance of precise spike arrival times, such as provided by frequency and phase locked spike trains, is not required. At present, there is a good deal of evidence supporting mean rate codes in various neural structures (Perkel and Bullock, 1968). The next section deals with the neural holographic processes that are possible using such codes.

Neural Holographic Processes

Linear Codes

Since incoming spike trains are most likely of varying frequencies with some component of random fluctuation in each, it is improbable that a stable temporal interaction can be achieved at the level of individual spike arrivals. The interference pattern must therefore be defined in terms of some time-averaged parameter. Mean rate, the average spike arrival rate within some time interval, appears to serve the required purpose. The first important attribute of the mean rate description of neural activity is that a neuron is a relatively linear transducer of this parameter for irregular (Poisson) excitatory or inhibitory input (Enger, et al., 1969; Perkel, et al., 1964). The mean rate output of a neuron thus responds linearly to the algebraic sum of the mean rates of multiple inputs (assuming the inputs are independent—Segundo, et al., 1968) over the range delimited by the suppression of the neuron's output and its maximum firing rate. If adjacent cells are interrelated in some manner, the processing elements of the neural system are more accurately the ensembles of interdependent cells; the linear operating regions of such ensembles may be considerably greater than that of the constituent neurons, depending on the distribution of the individual ranges. (Whether the processing elements are individual cells or groups of interrelated cells, they can be represented conceptually as single neurons with no loss in generality.) The property of linearity leads to great simplification in the mathematical description of the system—a simplification that is also enjoyed in optical holography by virtue of the linearity of the wave equations describing the propagation of light through most media.

The second and most important attribute of the mean rate parameter is that its use in various forms as a code for stimulus properties has been demonstrated in many neural struc-tures (Perkel and Bullock, 1968). The two forms of mean rate coding most prevalent in the brain are frequency modulation or mean rate modulation (MRM) and directional rate change

DRC, most frequently called simply mean rate coding, but it will be labelled differently here to emphasize that frequency modulation is also a mean rate code . Although other codes have been identified[1], the analysis of neural holographic processes will center on these two. Both involve a base rate of random firing; MRM implies a periodic oscillation of the mean rate about the base level and is a candidate code wherever periodicity is found— e.g., the theta rhythm (4-7 Hz) in the hippocampus, the alpha (8-13 Hz) in the thalamus and cortex, and beta (20-30 Hz) in the cortex; DRC is the classical code for stimulus intensity and involves a continuing increment of decrement in the mean firing rate about the base level as shown by De Valois, et al. (1962) in the lateral geniculate.

The MRM code can be represented by a cosine function:

$$\text{mean rate} = r + M\cos(2\pi ft + \theta) \tag{4}$$

> r – the base rate
> M – amplitude of deviation from base rate
> f – frequency of modulation
> t – time
> θ – phase of the particular spike train relative to some reference

For the MRM code to be meaningful in a neural holographic process, there must be a single generator of the carrier frequency (a pacemaker) that modulates all the spike trains involved. Thus, f will be the same for all spike trains and θ, the phase of the modulation for each train, will be with respect to a common reference.

The DRC code can be expressed in terms of a binary function, denoted evn, representing the direction—increment or decrement—of the change in mean rate.

$$\text{evn}\theta = (-1)^{\theta} \qquad \theta - \text{the direction index, taking integer values}$$
$$\text{mean rate} = r + M\,\text{evn}\theta \qquad r, M - \text{as before} \tag{5}$$

Thus the mean rate increases by M if the direction index, θ, is even and decreases by M if it is odd. The direction index is in some respects analogous to phase; unlike phase, however, it is a discontinuous dimension.

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[1] Mean rate codes are, in general, the most suitable for holographic purposes. If more than one type of code supports storage and reconstruction, it might be possible to superimpose the various codes (assuming they are orthogonal) and simultaneously store and retrieve independent information wavefronts in the same storage area. Distribution coding, although it has been frequently observed (Perkel and Bullock, 1968), is an improbably candidate for significant holographic processing. First of all, with many weak, independent synaptic inputs (which must be assumed for redundant storage to occur), the distribution of output firing bears no relation to input distributions (Segundo, et al., 1968). Second, even under the condition of a limited number of relatively strong inputs, storage and retrieval of distribution parameters other than the mean is possible only in a number of special cases.

The natural occurrence of these two mean rate codes makes the requirements for holographic storage far less restrictive in the neural case than in the optical. The structural coherence of the fixed interneural connections and the time-averaged property of the codes for which neurons are linear transducers permit a stable spatio-temporal interaction of wavefronts that have no fixed frequency or phase relations. It remains to be demonstrated, however, that the neural interference patterns can be stored isomorphically by some process of neuronal change. Before confronting this task, the neural structure required for holographic processes will be analyzed.

Neural Representation of Symbolic Information

The two codes described above characterize single spike trains. A neural wavefront is simply a spatial array of spike trains and will be considered the mode of representation for symbolic information in the brain (stimulus patterns, concepts, motor commands, etc.).

Figure 2 depicts a possible structure for a neural holographic system. a and b are input wavefronts that map through transforms X and Y, respectively, onto the storage field
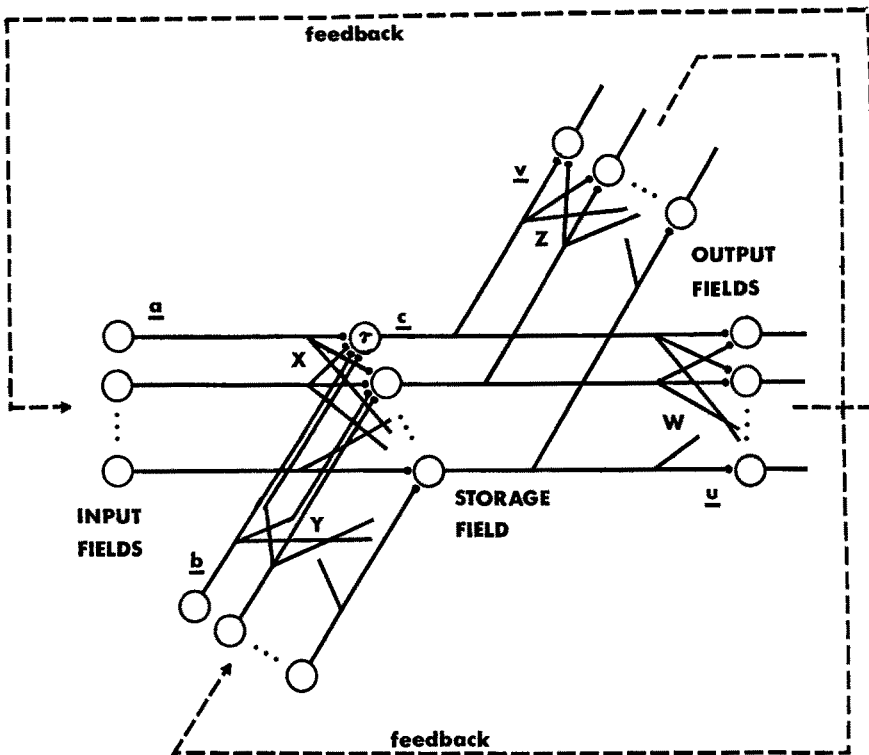

FIGURE 2: A possible structure for a holographic neural system.

neurons. τ is the diagonal matrix of transmission coefficients expressing the linear relation between the algebraic sum of the inputs to each neuron and the mean output rate of each neuron—i.e., τ represents the efficiency with which input rate variations affect output rate variations. W and Z map this output $\underline{c}$ onto $\underline{u}$ and $\underline{v}$. The transforms X, Y, W, and Z are such that with no information recorded in the storage area, $\underline{a}$ and $\underline{b}$ are able to cross through each other and end up separately in $\underline{u}$ and $\underline{v}$, respectively. $\underline{a}$, in other words, produces no output in $\underline{v}$ and $\underline{b}$ no output in $\underline{u}$. Simultaneously exposing the storage field to $\underline{a}$ and $\underline{b}$ alters the transmission coefficients of these neurons in proportion to the interference pattern of $\underline{a}$ and $\underline{b}$. The spatial variations of τ which code this interference pattern now allow wavefront $\underline{a}$ to produce output in $\underline{v}$ which, it will be shown, is a reconstruction of $\underline{b}$'s output to $\underline{u}$. Thus, the spatial variations of τ are the neural hologram.

Expressing these relations mathematically:

$$\underline{u} = W\underline{c} \tag{6}$$

$$\underline{v} = Z\underline{c} \tag{7}$$

$$\underline{c} = r_c + \tau(X\underline{a} + Y\underline{b}) \tag{8}$$

$$\underline{A} = X\underline{a} \tag{9}$$

$$\underline{B} = Y\underline{b} \tag{10}$$

$\underline{}$ – denotes that the elements of the variable are coded spike trains

$\underline{a}, \underline{b}$ – input wavefronts (column vectors) of discrete pulse trains

$\underline{u}, \underline{v}$ – wavefronts arriving at the two output fields (column vectors)

$\underline{c}$ – wavefront output from the storage field neurons

W, X, Y, Z – transform matrices of synaptic coupling coefficients

$\underline{A}, \underline{B}$ – the input wavefronts at the storage field (column vectors)

r_c – column vector of the base firing rates of the storage field neurons

τ – diagonal matrix of transmission coefficients of storage field neurons

Initially τ is a scalar matrix (although this is not a necessary assumption, it simplifies analysis).

$$\tau = \lambda I$$

$$\underline{u} = Wr_c + W\tau(X\underline{a} + Y\underline{b}) = Wr_c + W\lambda IX\underline{a} + W\lambda IY\underline{b}$$

$$\underline{u} = Wr_c + \lambda(WX\underline{a} + WY\underline{b}) \qquad ; \tag{11}$$

similarly,

$$\underline{v} = Zr_c + \lambda(ZX\underline{a} + ZY\underline{b}) \tag{12}$$

For $\underline{a}$ to produce output only in $\underline{u}$ and $\underline{b}$ only in $\underline{v}$,

$$WY = 0 , \qquad ZX = 0 \quad . \tag{13}$$

After recording, the transmission coefficients have been altered in some manner. These $\Delta\tau$'s are variable across the storage field. For reconstruction, $\underline{a}$ is again input, but $\underline{b}$ is zero (ignoring base rates).

$$v = Z\tau X\underline{a} = Z(\bar{\tau}I + \Delta\tau)X\underline{a} = Z\bar{\tau}I\underline{a} + Z\Delta\tau X\underline{a} = \bar{\tau}ZX\underline{a} + Z\Delta\tau X\underline{a} \tag{14}$$

$\bar{\tau}$ – average value of τ
$\Delta\tau$ –diagonal matrix of variations of τ around $\bar{\tau}$

$$ZX = 0$$
$$\underline{v} = Z\Delta\tau X\underline{a} \tag{15}$$

Any term in τ, therefore, that is constant over all storage neurons does not generate any output in the reconstruction field. Thus, $\Delta\tau X\underline{a}$ must contain $Y\underline{b}$ (i.e., $\Delta\tau\underline{A}$ must contain $\underline{B}$) if an accurate reconstruction is to be produced.

The relations between W and Y and Z and X expressed in equation (13) are essential to the processing of the neural wavefronts and are analogous to the recording geometries in optical holography that allow separation of output images. It is possible, because of their importance to processing, that these relations have developed through evolution; conversely, $\underline{u}$ and $\underline{v}$ may simply be the subset of output fields of the storage neurons whose transforms obey these relations.

The feedback loops shown in Figure 2 illustrate that this structure could be two circulating neural nets that intersect at a set of modifiable neurons. The association between the various "cell assemblies" (Hebb, 1949) realizable in the nets thus occurs at their intersection.

Finally, in analyzing the storage and reconstruction, only the wavefronts at the storage field, $\underline{A}$ and $\underline{B}$, need be considered as these are the wavefronts that directly produce the interference pattern to be stored. The expressions for $\underline{A}$ and $\underline{B}$ are, for MRM coding, where the subscript i indicates input activity at the ith storage neuron:

$$\underline{A} = X\underline{a} = \left[r_{Ai} + A_i \cos(2\pi ft + \theta_i)\right] \tag{16}$$

$$\underline{B} = Y\underline{b} = \left[r_{Bi} + B_i \cos(2\pi ft + \phi_i)\right] \tag{17}$$

and for DRC coding,

$$\underline{A} = X\underline{a} = \left[r_{Ai} + A_i \operatorname{evn}\theta_i\right] \tag{18}$$

$$\underline{B} = Y\underline{b} = \left[r_{Bi} + B_i \operatorname{evn}\phi_i\right] \tag{19}$$

Models of Neuronal Change

At present, the basis of neuronal change is unknown, but there are a number of hypotheses of the factors that might lead to such change (Kupfermann and Pinsker, 1969) and these fall into two main classes. The first states that the degree of usage of the synaptic terminals or of the postsynaptic cell somehow affects their subsequent efficiency. The second proposes that the concurrence of action potentials at the pre- and postsynaptic membranes and the consequent permeability of both, allows some form of molecular communication that effects a change in transmission efficiency; the probability of concurrence at each synapse will depend both on the output rate of the postsynaptic cell and on the input rate at the synapse.

To allow holographic storage, the neuronal change must code the linear interaction of the two inputs $\underline{A}$ and $\underline{B}$ (i.e., $\underline{A} + \underline{B}$). This requirement is met by the postsynaptic use and concurrent use hypotheses, both of which reflect the output rate $(\underline{A} + \underline{B})$ of the postsynaptic cell; the synaptic use hypothesis, however, reflects only the input to each particular synapse and so cannot support holographic processes. Furthermore, since the inhibitory and excitatory components of an input cancel in their effect on the output of the postsynaptic cell, isomorphic coding requires that their effects on the transmission efficiency of a cell also cancel. This is satisfied by the postsynaptic use hypothesis (simple use) where neuronal change is a function only of the output rate of the postsynaptic cell. In the case of concurrent use, the agent of neuronal change is the substance passing between pre- and postsynaptic processes and this interchange is a function not only of postsynaptic firing but also of the input rates at each synapse. For the molecular agents of inhibitory and excitatory inputs to counteract each other, they must be mutually antagonistic and must be able to diffuse and interact, even if only on a local basis (assuming random spatial distribution of inputs), after passing across the postsynaptic membrane. If input to each cell is either all inhibitory or all excitatory, this cancellation requirement is, of course, unnecessary and the transport can be in either direction across the synaptic cleft (this form of the concurrence hypothesis is typically called specific use).

Finally, it can be shown that when the function expressing neuronal change (the transmission function) contains linear terms in $\underline{A}$ or $\underline{B}$, significant noise results in the reconstruction field. Since MRM coding is periodic, any linear terms will average to zero over one period; DRC coding, however, is not time varying and linear terms can only be suppressed in the concurrence hypotheses with certain restrictions and cannot be suppressed at all in the simple use case (requiring, therefore, the absence of linear terms, and, in fact, all odd-powered terms, in the transmission function).

To summarize the properties of the various hypotheses: holographic storage of MRM coded input is supported by simple and concurrent use and by specific use when input to each cell is either all excitatory or inhibitory; holographic storage of DRC coded input is possible for special cases of simple and specific use; the change in neuronal transmission efficiency (τ) involves the cell as a unit in simple use, local areas of the cell in concurrent use (in both cases, the change affects all input to the cell equally), and individual synapses in specific use.

The neural holographic process will be analyzed for the case of concurrent use where each concurrence contributes equally to the change in transmission efficiency. Although any number of other models could have been chosen for analysis, this particular model has a number of advantages: it offers more structure and fewer restrictions than the simple use model; it applies equally to processing units of single cells or ensembles of cells; the equality of the effect of each concurrence is intuitively attractive; the results generalize readily to the specific use model; and behavioral data discussed in the latter half of this paper show that the transmission function must be an exponential (Cavanagh, 1972) and such a function is a fundamental characteristic of the model to be considered.

The selected model postulates that concurrent use leads to change, but change in what direction? Most experimental evidence, especially in the peripheral nervous system, suggest that use weakens, rather than strengthens, the transmission efficiency of a cell when input is excitatory (Sharpless, 1964). Such a change is compatible with the phenomena of habituation, extinction, and spontaneous recovery, among others. Griffiths (1966) has demonstrated how this weakening acts as negative feedback to stabilize neuron output; if, conversely, use led the strengthening, the concomitant positive feedback would produce instability or runaway in the cell's output.

No experimental work has been done on the effects of inhibitory input. However, to obtain the same stability, concurrence of the postsynaptic action potential with the arrival of inhibitory impulses must lead to strengthening of the effectiveness of inhibitory input. If weakening (i.e., release from inhibition) were to result, the cell's output would again increase autonomously.

The concurrence of action potentials at a synapse must affect not only the synapse involved but also neighboring synapses which may be of similar or different nature. This can be accomplished if the molecular agent released by an inhibitory concurrence strengthens, and that released by an excitatory concurrence weakens, the receptor sensitivity of either type of synapse. These two actions are then also mutually antagonistic, as previously required. Since the model is addressing short term memory processes with a time scale in the order of seconds, such changes in receptor sensitivity (assuming excitatory input) might be seen on a gross level as fatigue or accommodation, a consistently observable cellular phenomenon.

Various assumptions have been made concerning the mechanisms of neuronal change and the analysis of holographic storage and retrieval will now be undertaken based on these assumptions. It must be emphasized that the feasibility of holographic processes does not depend on these assumptions and that equivalent derivations result from a variety of other neuronal models.

Figure 3 shows a single neuron (chosen arbitrarily so that no subscripts will be used) where $\underline{A}$ represents the algebraic sum of input from the $\underline{a}$ wavefront and $\underline{B}$ the sum from the $\underline{b}$ wavefront.

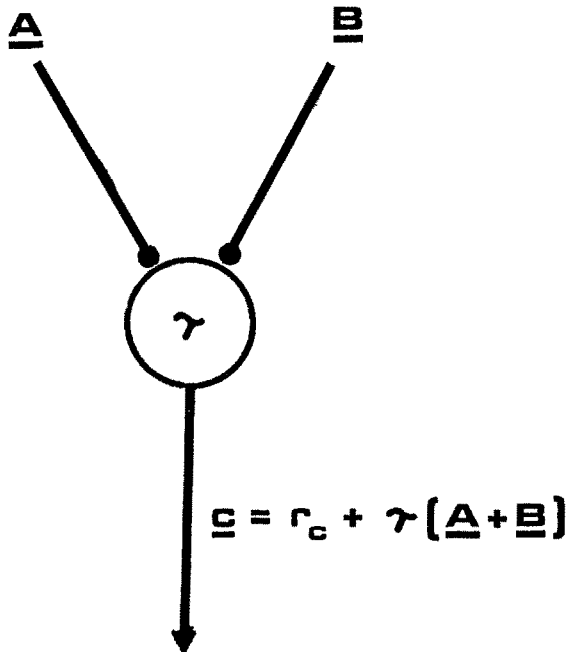$$\underline{c} = r_c + \gamma \left(\underline{A} + \underline{B} \right)$$

FIGURE 3: A single neuron in the storage field. $\underline{A}$ and $\underline{B}$ are the sums of all the input effects from $\underline{a}$ and $\underline{b}$ respectively.

Considering the MRM code, when the total synaptic effect is positive, then the output of the cell is in phase with the input. With multisynaptic input, the input and output processes can be considered independent[1] with linearly related means. The expected number of concurrent pre- and postsynaptic action potentials (hits) per unit time is then directly proportional to the product of the mean input and output rates.

$$E(hit) = E\left\{ (r_c + \tau(\underline{A} + \underline{B})) \cdot (\underline{A} + \underline{B}) \right\} . \tag{20}$$

E - expected value

Assuming that the duration of exposure, t, is a random variable unrelated to the period of the modulating wavefront, the expected number of hits can be estimated by averaging over one period,

$$E(hit) = \frac{1}{2\pi} \int_0^{2\pi} \Big(r_c + \tau\big(r_A + r_B + A\cos(2\pi ft + \theta) + B\cos(2\pi ft + \phi)\big)\Big)$$

$$\cdot \big(r_A + r_B + A\cos(2\pi ft + \theta) + B\cos(2\pi ft + \phi)\big)\, d(2\pi ft)$$

$$E(hit) = \tau(r_A + r_B)^2 + r_c(r_A + r_B) + \tau(A^2 + B^2 + 2AB\cos\gamma) \tag{21}$$

where $\gamma = \theta - \phi$.

γ - phase difference between the two inputs

If each hit contributes an equal amount to the weakening of the transmission efficiency, then the rate of change of τ will be linearly related to E(hit). Assuming an equilibrium process that maintains τ at a steady level when there is no input other than the base rates, the expression is

$$\frac{d\tau}{dt} = -\alpha E(hit) + \alpha\Big(\tau(r_A + r_B)^2 + r_c(r_A + r_B)\Big)$$

$$= -\alpha\tau(A^2 + B^2 + 2AB\cos\gamma) \tag{22}$$

Integrating over t, the total time for which the storage neuron is exposed to $\underline{A}$ and $\underline{B}$,

$$\tau = \lambda e^{-\alpha t(A^2 + B^2 + 2AB\cos\gamma)} \tag{23}$$

α, λ - constants.

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[1] While an arriving spike may initiate an action potential (or suppress an imminent one in the case of inhibitory input) at or near the receiving postsynaptic site, this spatio-temporal input-output dependence only occurs with significant frequency for the few synapses near the axon hillock. With the number of input processes in the order of thousands (10,000 synapses is typical in the cortex), the majority of spatio-temporally simultaneous pre- and postsynaptic action potential arrivals will occur as the postsynaptic action potential sweeps through the dendritic tree. Thus, for determining the rate at which these even are achieved, the input and output processes are effectively independent.

If the total synaptic effect is inhibitory, the output $\underline{c}$ will decrease when input $(\underline{A} + \underline{B})$ increases. Therefore

$$E(\text{hit}) = E\left\{\left(r_c - \tau(\underline{A} + \underline{B})\right) \cdot (\underline{A} + \underline{B})\right\} \qquad (24)$$

and the average, as in equation (21), over one period is

$$E(\text{hit}) = -\tau(r_A + r_B)^2 + r_c(r_A + r_B) - \tau(A^2 + B^2 + 2AB\cos\gamma) \quad . \qquad (25)$$

However, each hit now contributes to the increase of τ. Again, with an equilibrium process,

$$\frac{d\tau}{dt} = +\alpha E(\text{hit}) + \alpha\left(\tau(r_A + r_B) - r_c(r_A + r_B)\right) = -\alpha\tau(A^2 + B^2 + 2AB\cos\gamma) \quad ;$$

again, $\tau = \lambda e^{-\alpha t(A^2 + B^2 + 2AB\cos\gamma)}$.

As expected, both excitatory and inhibitory input (and therefore any combination of the two) lead to the same storage characteristic. α represents the storage parameter, the strength with which incoming information alters the cell. λ is simply the base level of τ with no information stored and t represents the exposure time of the input. The elements of $[\tau]$, the diagonal matrix of transmission coefficients that codes the neural hologram, are given by

$$\tau_{ii} = \lambda e^{-\alpha t(A_i^2 + B_i^2 + 2A_i B_i \cos\gamma_i)}$$

For the DRC code, there are limitations on the interneural connections and base firing rates that will allow useful storage. The restrictions are that the total synaptic effect must be inhibitory and that the base rates are related as follows:

$$r_c = 2(r_A + r_B) \quad . \qquad (26)$$

In electrical engineering terms, equation (26) places the quiescent point midway in the operating range of the neuron. It is the optimum operating point in that it allows the maximum signal input without distortion; nevertheless, it is a definite restriction on the generality of the model. The expected rate of hits in this case is

$$E(\text{hit}) = -\tau(r_A + r_B)^2 + r_c(r_A + r_B) + \left(r_c - 2\tau(r_A + r_B)\right) \cdot (\text{Aevn}\theta + \text{Bevn}\phi)$$
$$- \tau(\text{Aevn}\theta + \text{Bevn}\phi)^2 \quad .$$

Because of the restriction of equation (26), this reduces to

$$E(\text{hit}) = -\tau(r_A + r_B)^2 + r_c(r_A + r_B) - \tau(\text{Aevn}\theta + \text{Bevn}\phi)^2 \quad . \qquad (27)$$

Thus the combined effect of the two restrictions is to eliminate the first order terms of evnθ and evnϕ. It can be shown that these terms make any useful reconstruction of information impossible.

The rate of change of τ is now

$$\frac{d\tau}{dt} = \alpha E(\text{hit}) + \alpha\left(\tau(r_A + r_B)^2 - r_c(r_A + r_B)\right) = -\alpha\tau(A\text{evn}\theta + B\text{evn}\phi)^2 \; ;$$

since $(\text{evn}\theta)^2$, $(\text{evn}\phi)^2 = 1$
and $\text{even}\theta \cdot \text{evn}\phi = \text{evn}(\theta - \phi)$,

$$\frac{d\tau}{dt} = -\alpha\tau(A^2 + B^2 + 2AB\text{evn}\gamma) \tag{28}$$

where $\gamma = \theta - \phi$;

thus

$$\tau = \lambda e^{-\alpha t(A^2 + B^2 + 2AB\text{evn}\gamma)} \tag{29}$$

and

$$\tau_{ii} = \lambda e^{-\alpha t(A_i^2 + B_i^2 + 2A_i B_i \text{evn}\gamma_i)}$$

Both codes have led to the conclusion of an exponential storage characteristic. That is, the transmission coefficients of the neurons which encode the interference pattern of the two wavefronts vary exponentially with the input signals. It has been shown optically (Friesem and Zelenka, 1967) that reconstruction is possible with nonlinear recording characteristics. The main effect of the nonlinearity is to produce the higher order images analogous to the higher order diffractions from an optical grating. These unwanted images can typically be separated from the desired reconstruction.

At present, no analysis of the possibility of decay of stored information will be made, as it does not play an important role in the behavioral tasks to which the model will be applied. The mechanism of storage implies that there may be an exponential decay although this is not strictly true. The information might remain unchanged over time until some external control signal effectively causes it to be erased. In a similar manner, a control signal might also govern the recording of information, increasing the value of α (equations (23) and (29)) to store interference patterns and decreasing α to ignore them.

Reconstruction

Having developed expressions for τ, the form of the reconstructed wavefront can now be determined. Initially, the amplitude moduli, A and B, will be assumed constant for each neuron to simplify the derived expressions; the effect of relaxing this assumption is analyzed at the end of this section.

To obtain reconstruction after the interference pattern of $\underline{A}$ and $\underline{B}$ has been stored, $\underline{A}$ alone or $\underline{B}$ alone is input to the storage field.

MRM Code. Considering reconstruction with the input of the $\underline{A}$ wavefront, output at an arbitrary neuron is

$$\underline{c} = r_c + \lambda e^{-\alpha t(A^2 + B^2 + 2AB\cos\gamma)} \cdot \left(r_A + r_B + A\cos(2\pi ft + \theta)\right) \ . \tag{30}$$

As demonstrated by Tokarski (1968) in the optical case, the transmission coefficient can be expanded in a Fourier cosine series to determine the image producing term,

$$\underline{c} = r_c + \left(r_A + r_B + A\cos(2\pi ft + \theta)\right) \cdot \left(\lambda \sum_0^\infty T_m \cos(m\gamma)\right) \tag{31}$$

$$T_m, \quad m = 0, 1, 2, \ldots \text{ - Fourier coefficients.}$$

Only the term for $m = 1$ will contain a replica of the $\underline{B}$ wavefront, all terms for $m > 1$ produce higher order images. The $m = 0$ term is a constant. The first two Fourier coefficients are

$$T_0 = \frac{1}{2\pi} \int_0^{2\pi} e^{-\alpha t(A^2 + B^2 + 2AB\cos\gamma)} d\gamma = e^{-\alpha t(A^2 + B^2)} \cdot 1_0(2\alpha tAB) \tag{32}$$

$$1_0 \text{ - zero order modified Bessel function,}$$

$$T_1 = \frac{1}{\pi} \int_0^{2\pi} e^{-\alpha t(A^2 + B^2 + 2AB\cos\gamma)} \cdot \cos\gamma d\gamma = -2e^{-\alpha t(A^2 + B^2)} \cdot 1_1(2\alpha tAB) \tag{}$$

$$1_1 \text{ - first order mofified Bessel function;}$$

thus

$$\underline{c} = r_c + (r_A + r_B)\lambda\left(\sum_0^\infty T_m\cos(m\gamma)\right) + A\cos(2\pi ft + \theta)\lambda e^{-\alpha t(A^2 + B^2)} 1_0(2\alpha tAB)$$

$$- A\cos(2\pi ft + \theta)\left(2\lambda e^{-\alpha t(A^2 + B^2)} \cdot 1_1(2\alpha tAB)\right)\cos\gamma + \text{higher order terms} \tag{34}$$

In equation (34): r_c will produce the base firing rates at the output field; $r_A + r_B$ and $\cos m\gamma$ are independent and so will generate a randomly distributed noise field that is subsumed in the base rates at $\underline{v}$; the third term is constant for all the neurons of the storage field so that there is no output in $\underline{v}$ as a result of this term (equations (14) and (15)); the fourth term is the reconstruction term; the higher order terms propagate to $\underline{v}$, but, analogous to the optical case, can be separated from the desired reconstruction by the transform Z. The recon-

struction term is then

$$c_r = -\lambda a e^{-\alpha t(A^2 + B^2)} 1_1(2\alpha tAB) \left(2\cos(2\pi ft + \theta) \cdot \cos\gamma\right)$$

but $\gamma = \theta - \phi$

$$c_r = -\lambda A e^{-\alpha t(A^2 + B^2)} 1_1(2\alpha tAB) \left(\cos(2\pi ft + \phi) + \cos(2\pi ft + 2\theta - \phi)\right) . \tag{35}$$

Since amplitude moduli were assumed constant, only the phase of the B wavefront need be recovered for reconstruction. This is the case in equation (35), the first cosine term being the phase of B. The leading terms represent the amplitude of the B reconstruction; the second cosine term is the complement of B and is similar to the conjugate image in optical holography.

Thus a linear reconstruction of the B wavefront has been obtained (the linearity is partially a result of the assumption of constant amplitude moduli) allowing the conclusion that neural holography can be achieved using this very general mean rate modulation code. The complementary and higher order reconstructions are equivalent to the multiple images produced in optical holography. It is reasonable to assume that these can be separated from the desired reconstruction given the appropriate anatomy of the neural structure.

DRC Code. The analysis of reconstruction with the DRC code leads to a rather significant result. Considering again input of the A wavefront alone, equations (ठ) and (29) give

$$\underline{c} = r_c - (r_A + r_B + Aevn\theta)\lambda e^{-\alpha t(A^2 + B^2 + 2ABevn\gamma)} .$$

Expanding the variable part of the exponential,

$$\underline{c} = r_c - (r_A + r_B + Aevn\theta)\lambda e^{-\alpha t(A^2 + B^2)} \cdot \left\{1 - 2\alpha tABevn\gamma + \frac{(2\alpha tABevn\gamma)^2}{2!} - \dots\right\} ,$$

but $(evn\gamma)^{2n} = 1$

and $(evn\gamma)^{2n+1} = evn\gamma ,$ n - any integer

$$\underline{c} = r_c - (r_A + r_B + Aevn\theta)\lambda e^{-\alpha t(A^2 + B^2)} \cdot \left\{1 + \frac{(2\alpha tAB)^2}{2!} + \frac{(2\alpha tAB)^4}{4!} + \dots \right.$$

$$\left. -(2\alpha tAB)evn\gamma - \frac{(2\alpha tAB)^3}{3!}evn\gamma - \frac{(2\alpha tAB)^5}{5!}evn\gamma - \dots\right\}$$

$$\underline{c} = r_c - (r_A + r_B + Aevn\theta)\lambda e^{-\alpha t(A^2 + B^2)} \cdot \left(\cosh(2\alpha tAB) - \sinh(2\alpha tAB)evn\gamma\right) \tag{36}$$

$$\underline{c} = r_c - (r_A + r_B + A\operatorname{evn}\theta)\lambda e^{-\alpha t(A^2 + B^2)}\cosh(2\alpha tAB)$$

$$+ (r_A + r_B)\lambda e^{-\alpha t(A^2 + B^2)}\sinh(2\alpha tAB)\operatorname{evn}\gamma$$

$$+ \lambda A e^{-\alpha t(A^2 + B^2)}\sinh(2\alpha tAB)\operatorname{evn}\theta\operatorname{evn}\gamma \tag{37}$$

r_c is again the base rate; the second term contains the direct transmission coefficient which is constant for all neurons and therefore allows propagation to $\underline{u}$ but not to $\underline{v}$; in the third term $r_A + r_B$ and $\operatorname{evn}\gamma$ are independent variables and thus produce randomly distributed noise in $\underline{v}$; the fourth term is the reconstruction term.

$$c_r = \lambda A e^{-\alpha t(A^2 + B^2)}\sinh(2\alpha tAB)\operatorname{evn}\theta\operatorname{evn}\gamma \ ;$$

but $\operatorname{evn}\theta \cdot \operatorname{evn}\gamma = \operatorname{evn}(\theta - \gamma)$

and $\gamma = \theta - \phi$

$$c_r = \lambda A e^{-\alpha t(A^2 + B^2)}\sinh(2\alpha tAB) \cdot \operatorname{evn}\phi \quad . \tag{38}$$

The direction dimension of the $\underline{B}$ wavefront is recovered ($\operatorname{evn}\phi$) and since amplitude moduli were assumed constant, $\underline{B}$ has been linearly reconstructed. The important result is that only one wavefront component is generated; the complement of $\underline{B}$ is not produced nor are higher order images, even though the recording is nonlinear (this result will hold for any form of nonlinearity). This simplicity in the output space, which cannot be obtained in the optical or neural MRM cases, permits a great deal of generality in the neural anatomies appropriate for holographic processes.

The Effect of Variable Amplitude Moduli. The previous sections have dealt with storage and reconstruction with the assumption of a constant amplitude of input to each neuron. The information stored and recovered was that of phase or direction. Allowing the amplitude moduli, A and B, to vary over the storage neurons increases the amount of information that can be represented, while still permitting the faithful recovery of phase or direction. It is not possible, however, to recover the amplitude terms without a certain amount of noise and distortion. Since the condition of strictly constant moduli is unlikely in the brain, it is important to determine the form of the resulting distortion.

Examination of equations (34) and (37) shows that there are three sources of distortion. First, the terms $\left\{\lambda e^{-\alpha t(A^2 + B^2)}I_0(2\alpha tAB)\right\}$, from equation (34), and $\left\{\lambda e^{-\alpha t(A^2 + B^2)}\cosh(2\alpha tAB)\right\}$, from equation (37), are the direct transmission coefficients.

As the constant terms in τ, they allow propagation to $\underline{u}$ but not to $\underline{v}$. With variable moduli, these expressions are no longer constants. Their spatial variation is independent of θ and ϕ and so produces a uniform noise output to $\underline{v}$ that increases in proportion to the variance of A and B. The effect of the noise depends on the ratio of the "area" in $\underline{v}$ to which the $\underline{B}$ wavefront propagates, to the total "area" reached by the noise. This ratio is determined by the output transform Z which could theoretically shrink the reconstruction "area" to minimize the effect of the noise.

The second source of distortion arises from the encoding of the amplitude in the product of an exponential and a Bessel (equation (34)) or a hyperbolic sine (equation (37)) function. To determine if the amplitude of $\underline{B}$ is recoverable, the products are expanded; from (34)

$$\alpha tA \cdot e^{-\alpha tA^2} \cdot \left\{ B - \alpha t \left(\frac{1 - \alpha tA^2}{2} \right) B^3 + \ldots \right\} \left(\cos\phi + \cos(2\theta - \phi) \right) \tag{39}$$

and from (37)

$$2\alpha tA \cdot e^{-\alpha tA^2} \cdot \left\{ B - \alpha t \left(\frac{1 - 2\alpha tA^2}{3} \right) B^3 + \ldots \right\} \text{evn}\phi \tag{40}$$

The expansions do contain first order terms in B. The first nonlinear term is cubic; however, the coefficient of this term can be made to equal zero with appropriate values of α, t and A.

The third source of distortion can be seen in equations (39) and (40). The terms to the left of the braces should be constant for a faithful reconstruction; the value of A, however, is variable. The variance of A around its mean value thus superimposes a random field of noise on top of the reconstructed $\underline{B}$ wavefront. Again there is a tradeoff between the increased information capacity with variable moduli and the resulting increase in noise.

These sources of noise and distortion are similar to those faced in optical holography where a careful choice of recording geometries and techniques usually suffices to minimize their effects. It is evident that if the brain were to use holographic storage, it too would have to make careful choices of neural transforms and signal codes; these choices could be made by natural selection in evolution.

In addition, the brain might have another mechanism to aid in noise suppression. If the neural holographic structure were two intersection networks as suggested previously, the self-seeking reverberations of such networks could act as feedback to suppress nonlinearities and random variability.

Storage of more than one interference pattern

It is possible for the neural hologram to record more than one interference pattern while still allowing separate retrieval of wavefronts from individual patterns. The equivalent optical case (multiple storage on two-dimensional holograms) has been analyzed by Collier and Pennington (1967); their study showed that reconstruction with no crosstalk is possible when the wavefronts being stored are uniquely coded—i.e., their cross-correlations with other wavefronts to be stored are minimal or zero. This result generalizes readily to the neural case as the wavefronts $\underline{A}$ and $\underline{B}$ vary uniquely over the storage field and can be assumed to have little correlation to subsequent sets of wavefronts being stored. Collier and Pennington reported that the crosstalk in this case is transformed into uniformly distributed noise that does not impair reconstruction.

Storage of multiple patterns in the neural case is achieved by the sequential exposure of the storage field to pairs of input wavefronts. For the MRM code then,

$$\tau = \lambda \exp \left(-\alpha \sum_{j=1}^{N} t_j (A_j^2 + B_j^2 + 2A_j B_j \cos \gamma) \right) ,$$

N – number of patterns stored.

Assuming that the wavefronts have the same average amplitude moduli and that exposure times are equal,

$$\tau = \lambda \exp \left(-\alpha N t (A^2 + B^2) - 2\alpha t A B \sum_{j=1}^{N} \cos \gamma_j \right) .$$

Expanding as the product of N Fourier cosine series (equations (32) and (33)),

$$\tau = \lambda e^{-\alpha N t (A^2 + B^2)} \cdot \prod_{j=1}^{N} \left\{ 1_0 (2\alpha t A B) - 2 1_1 (2\alpha t A B) \cos \gamma_j + \dots \right\}$$

$$\tau = \lambda e^{-\alpha N t (A^2 + B^2)} \cdot \left(1_0 (2\alpha t A B) \right)^{N}$$

$$- 2\lambda e^{-\alpha N t (A^2 + B^2)} \cdot \left(1_0 (2\alpha t A B) \right)^{N-1} \cdot \left(1_1 (2\alpha t A B) \right) \cdot \sum_{j=1}^{N} \cos \gamma_j$$

$$+ \text{ intermodulation and higher order terms} . \tag{41}$$

The first term is the direct transmission coefficient; the second is the reconstruction transmission coefficient—each $\cos \gamma_j$ contains the information for reconstruction of the jth wavefront. Intermodulation or crosstalk is produced, on input of the ith wavefront, by the cosine terms for $j \neq 1$ and by the terms containing products of two or more cosines.

Similarly for the DRC code,

$$\tau = \lambda \exp\left(-\alpha Nt(A^2 + B^2) - 2\alpha tAB \sum_{j=1}^{N} evn\gamma_j\right) \ .$$

Expanding as a product of N Taylor series (from equation (36)),

$$\tau = \lambda e^{-\alpha Nt(A^2 + B^2)} \cdot \prod_{j=1}^{N}\left\{\cosh(2\alpha tAB) - \sinh(2\alpha tAB) \cdot evn\gamma_j\right\}$$

$$\tau = \lambda e^{-\alpha Nt(A^2 + B^2)} \cdot \left(\cosh(2\alpha tAB)\right)^N$$

$$-\lambda e^{-\alpha Nt(A^2 + B^2)} \cdot \left(\cosh(2\alpha tAB)\right)^{N-1} \cdot \left(\sinh(2\alpha tAB)\right) \cdot \sum_{j=1}^{N} evn\gamma_j$$

$$+ \text{ intermodulation terms} \quad . \tag{42}$$

The terms are equivalent to those for the MRM code.

Notice in equations (41) and (42) that the reconstruction transmission coefficients have the same value for each of the N patterns. That is, the order of storage does not affect the amplitudes of the reconstructed wavefronts. This lack of a serial position effect would not have resulted if some form of storage decay had been assumed. Notice also that the amplitude of reconstruction decreases exponentially with the number of patterns stored. This implies that the transmission type neural hologram is a limited capacity store. Phase holography (Upatnieks and Leonard, 1970) does not attenuate amplitude as increasing numbers of patterns are stored and so might be a candidate model for a large capacity store such as long term memory.

Conclusions

A mathematical analysis has shown that holographic storage can be achieved in the neural domain for information coded in terms of mean rates; as this is a time-averaged parameter, it is possible for individual spike trains in a wavefront to vary randomly in instantaneous frequency and phase—a striking contrast to the strict frequency and phase requirements of optical holography. The properties of the neural holographic system were investigated for two classes of codes assuming, for convenience, a linear effect of concurrent pre-and postsynaptic impulses. Mean rate modulation (MRM) appeared more reasonable in terms of operating requirements, although the directional rate change code (DRC) did permit more flexibility in neural transforms. Finally, the neural hologram was shown to be capable of multiple storage of associations such that information from each individual association can be retrieved separately.

There could be many structures in the brain that are able to support these holographic processes. The configuration of input converging from two areas is, of course, widespread. It is only required that the neurons at the intersection be fatiguable for short term storage to occur. In addition, the two codes analyzed are found in many areas of the brain. On the other hand, however, it is a very difficult task to determine whether the appropriate transforms are available. Thus, while holography is a feasible storage process in the brain, the critical physiological test is beyond reach at present.

On the behavioral level, however, a range of powerful tests of the holographic hypothesis is possible and these are described in detail in a recent paper (Cavanagh, 1972). In brief, the paper postulates a short term memory system that stores the interference patterns between the wavefront of sensory information received from a stimulus and the wavefront that codes the internal information or "meaning" of the same stimulus. This arrangement allows rapid access recognition of sensory events and imaging of internal symbols (see Figure 4).[1]

The paper investigates reaction time (RT) predictions of the system for a recognition task developed by Sternberg (1966) in which a list of items is memorized and the reaction time to classify a test item as to list membership is measured. Since a test stimulus whose appropriate interference pattern has been stored (memorized) generates a reconstruction of its internal representation while a test stimulus with no stored pattern does not, the holographic system can classify stimuli as positive (stored) or negative (not stored) by monitoring output to the reconstruction area (Figure 5).

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[1] $\underline{A}$, the sensory representation, is assumed to be the end result of sensory processing, whatever the feature extractions or transformation that that may include. For example, in the visual system, $\underline{A}$ might be the output of area 19 of the visual cortex. The transforms required by the holographic system are simply those that allow separation of reconstructed images; no other properties are necessary to support storage and regrieval. Additional properties are required, however, to achieve the pattern recognition ability demonstrated by the brain. Kabrisky, et al. (1971) and Ginsberg (1971) have analyzed the various possible neural transforms that are in accord with human pattern recognition and perceptual illusions. It is not necessary that these be the transforms that map $\underline{A}$ onto the storage field neurons, they could equally well precede the production of the $\underline{A}$ wavefront. Finally, the analysis of the holographic recognition system assumes that X, Y, W, and Z are linear transforms with respect to the average amplitude of a wavefront. This implies that the column sums of each transform must be constant and allows the input ($\underline{a}$ and $\underline{b}$) and output ($\underline{u}$ and $\underline{v}$) wavefronts to be represented by the values of $\underline{A}$, $\underline{B}$, and $\underline{c}$ at a single arbitrary neuron in the storage field. This assumption simplifies analysis but is not essential in any way for holographic storage.
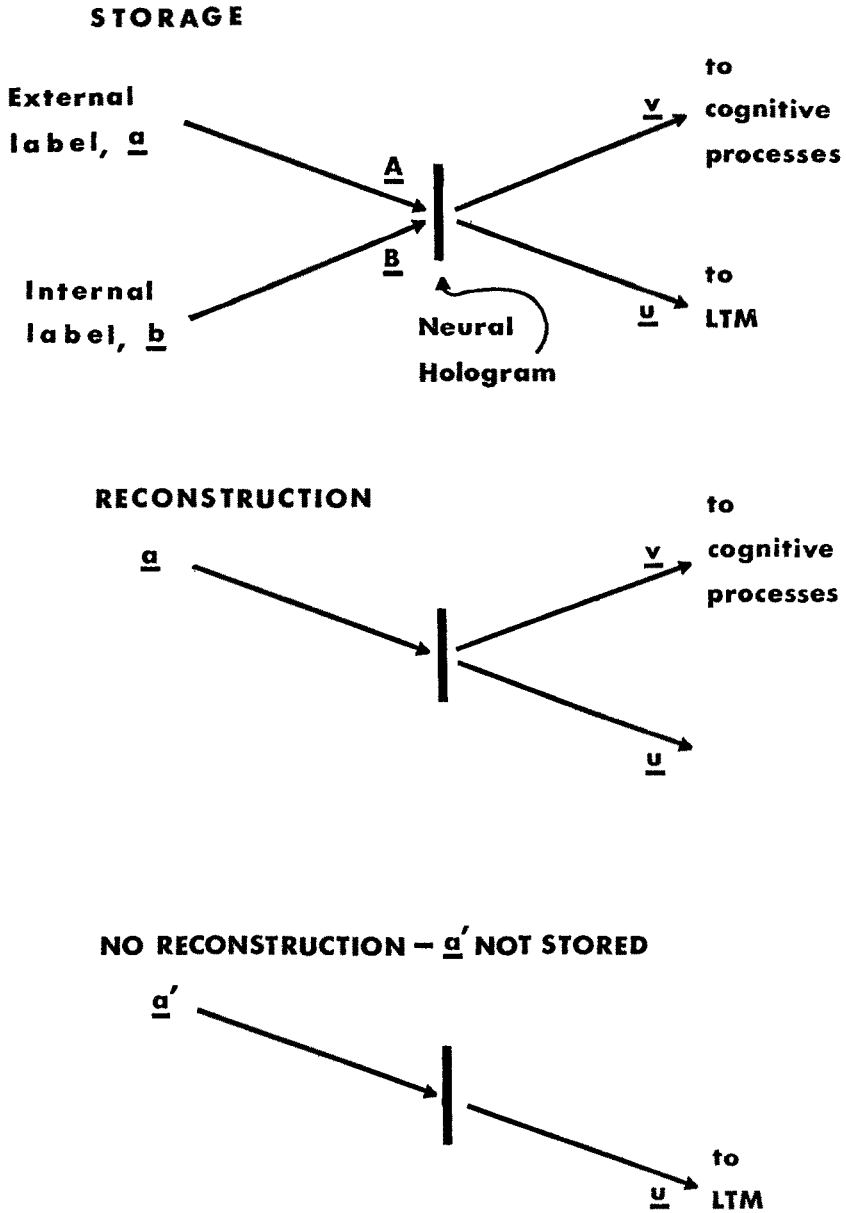
STORAGE

External
label, $\underline{a}$

$\underline{A}$

$\underline{v}$ to
cognitive
processes

$\underline{B}$

Internal
label, $\underline{b}$

Neural
Hologram

$\underline{u}$ to
LTM

RECONSTRUCTION

to

$\underline{a}$

$\underline{v}$ cognitive
processes

$\underline{u}$

NO RECONSTRUCTION – $\underline{a}'$ NOT STORED

$\underline{a}'$

$\underline{u}$ to
LTM

FIGURE 4: An holographic short term memory system. External information
is represented by wavefront propagation from input ($\underline{a}$) through
the storage field ($\underline{A}$) to the output field ($\underline{u}$), internal information,
by propagation from $\underline{b}$ through $\underline{B}$ to $\underline{v}$.

Reaction time components

t_s t_H t_{dr}, t_{do} t_R

I

log I/I_o A   gate $\mathcal{T}_r$ c_r d_r → Positive response

$\mathcal{T}_o$ inhibit c_o d_o → Negative response

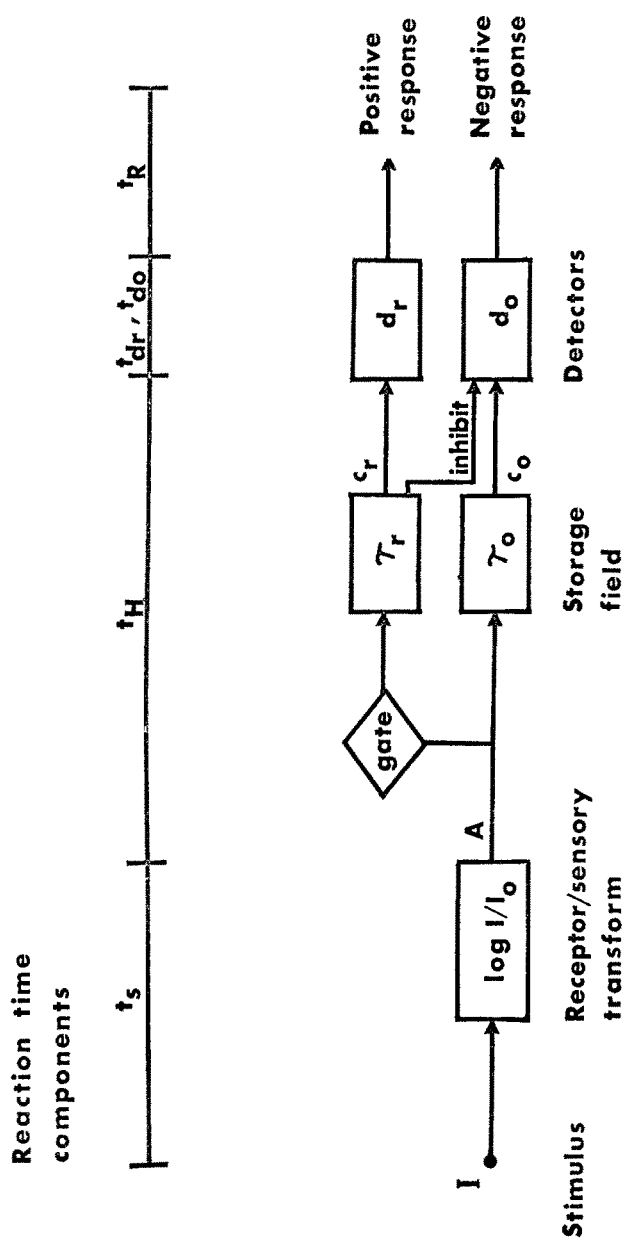Stimulus   Receptor/sensory transform   Storage field   Detectors

FIGURE 5: Schematic of system activity upon presentation of a test stimulus. The gate signifies that a reconstruction will occur only if the interference pattern appropriate to the test stimulus has been stored. The inhibitory input to the direct wavefront detector permits a positive response if the reconstructed wavefront is detected before the direct wavefront. A, c_r, and c_0 are wavefront amplitudes, I is the stimulus intensity and I_0 is the absolute threshold.

Sternberg's (1966) original results have been replicated many times, over a wide variety of conditions. Typical data for this item recognition task are shown in Figure 6.
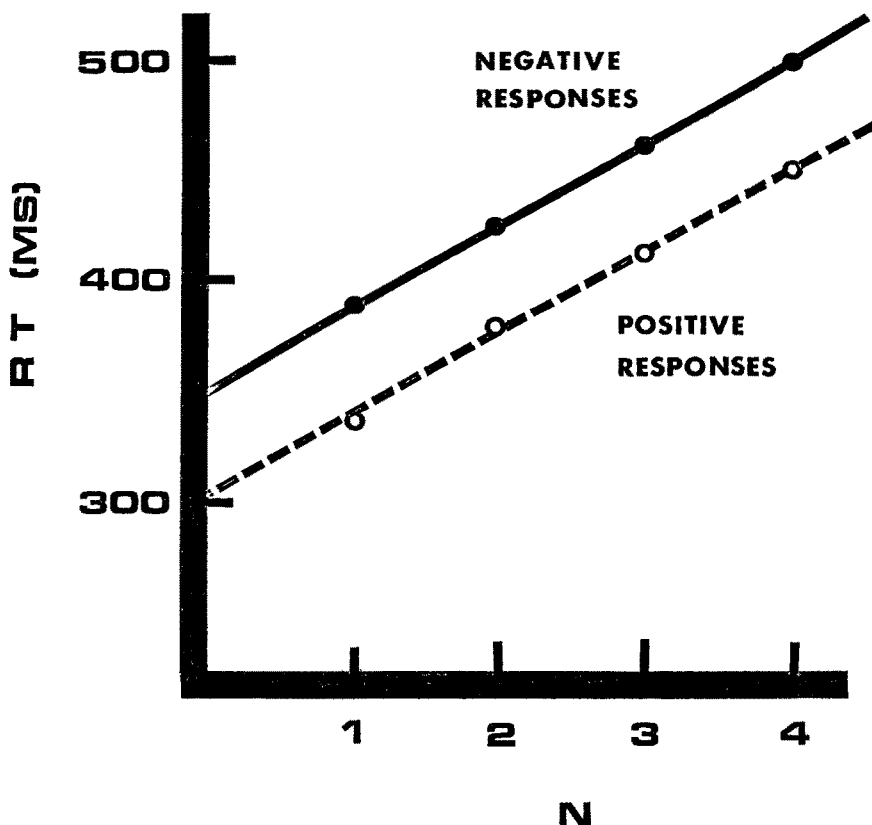

FIGURE 6: Typical reaction time results for the item recognition task.
N is the number of items memorized.

The important features of the data are the linear increase in reaction time with increasing length of the memorized list, the equality of the slopes (which are usually on the order of 30 to 40 ms per item) for positive and negative responses—i.e., response additivity, and a higher intercept for negative instances than positive. In the holographic model of the task, the locus of reaction time variation is taken to be the dependence of wavefront detection time (t_{do}, t_{dr}, see Figure 5) on wavefront amplitude. The amplitude of the storage field which was found from neurological derivations to be exponentially related to N, the number of items stored in memory. A mathematical derivation based on the experimentally observed response additivity also supports the exponential relation, justifying the concurrence model of neural change used in this paper. In addition, the additive effect of noise on reaction

time (Sternberg, 1967) leads to the conclusion of a logarithmic[1] detection function; this conclusion is confirmed by the relation between simple RT and stimulus intensity (99.9 percent of the variance of four simple RT studies—Cattell, 1866; Piéron, 1920; Bartlett and Macleod, 1954; Minucci and Connors, 1964—is accounted for by the logarithmic detection function in combination with a log energy transform at the receptor—Hartline and Graham, 1932). The concatenation of the logarithmic detection time vs. amplitude relation and the exponential amplitude vs. N relation predicts that reaction time is a linear function of the number of items memorized and that the slope of the function is the same for positive and negative responses with positives being uniformly faster than negatives. Furthermore, the assumption that the brain optimizes its processing capacity permits the slope of the RT function to be expressed in terms of the memory span for the type of material being tested. Data from the memory span and memory search literature supported the predicted reciprocal relation between span and processing rate (Cavanagh, in press).

Thus, on the behavioral level, the holographic hypothesis is supported without exception on a variety of measures. Investigation of the neural holographic process is underway at present on three additional levels: the possibility of long term memory based on phase holography or a two-stage "bleached" transmission holography; single cell recordings of the fatigue or habituation of neurons to confirm the behaviorally derived exponential relation; and, finally, the properties of complex information processing systems based on structures of interconnected holographic memories.

Acknowledgments

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[1] The logarithmic detection is very significant from another viewpoint. The neural holographic system that has been described is linear in terms of mean rates; a fundamental characteristic of random (Poisson) spike trains is, however, that the variance of the spike rate is linearly related to the mean. Thus, while the amplitude description of a wavefront is invariant over different absolute levels of firing (e.g., at different base rates, which change as τ changes during storage, or different directions of change—increase or decrease), the variance in which the amplitude information is submerged is variable. The logarithmic function is the one function that transforms the dependence of the variance on the mean to an invariance. The detectability of wavefronts is thus independent of absolute firing levels only in the case of logarithmic detection.

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