

(conceptual rather than molecular) conform to single time constant kinetics:

$$\tau(V)dp/dt + p = f(V)$$

where p is the probability a subunit is in the open conformation, and $\tau(V)$ and $f(V)$ describe the voltage dependent relaxation time constant and steady state probability of the subunit being open. $\tau(V)$ and $f(V)$ must be determined empirically from voltage clamp experiments. For the sodium channel, the subunit open probabilities are denoted by m and h (replacing p in the equation). The assumption that the activation subunits are identical and that all subunits open and close independently implies, then, that the sodium conductance is proportional to m^2h . For the potassium channel (where inactivation is neglected), the open probability is denoted by n (replacing p in the equation), and the assumption of four identical and independent subunits implies that the potassium conductance is proportional to n^4 . Modern treatments of channel behavior still often view subunits as being governed by a single relaxation time constant, but recent evidence indicates that the various subunits are not identical and independent so that the descriptive equations are more complex. The overall goal of all theories is still, however, to derive the coupling between subunits, and their relaxation time constants $\tau(V)$ and steady state open probabilities $f(V)$ as a function of voltage. As the structure of channel proteins becomes available, the goal will be to relate the Hodgkin and Huxley subunits to identified polypeptide chains, and to explain the rate constants in the Hodgkin and Huxley treatment

to molecular interactions that occur during conformational changes of the channel proteins. This process will probably take a number of years to complete.

See also Membrane Channels, Membrane Potentials; Squid Giant Axon

Further reading

Adrian RH, Chandler WK, Hodgkin AL (1970): Voltage clamp experiments in striated muscle fibres. *J Physiol* 208:607-644

Connor JA, Stevens CF (1971): Prediction of repetitive firing behaviour from voltage clamp data on an isolated neurone soma. *J Physiol (Lond)* 213:31-53

Dodge FA (1963): A study of ionic permeability changes underlying excitation in myelinated nerve fibers of the frog. PhD thesis, Rockefeller University. University Microfilms (No. 64-7333), Ann Arbor, Mich.

Hille B (1984): *Ionic Channels of Excitable Membranes*. Sunderland, Mass: Sinauer Associates

Hodgkin AL, Huxley AF (1952): A quantitative description of membrane current and its application to conduction and excitation in nerve. *J Physiol (Lond)* 117:500-544

McAllister RE, Noble D, Tsien RW (1975): Reconstruction of the electrical activity of cardiac Purkinje fibres. *J Physiol* 251:1-59

Partridge LD, Stevens CF (1976): A mechanism for spike frequency adaptation. *J Physiol* 256:315-332

Smith SJ (1978): The mechanism of bursting pacemaker activity in neurons of the mollusc *Tritonia diomedea*. PhD thesis. University of Washington, University Microfilms, Ann Arbor, Mich.

Holography and Brain Function

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There is considerable controversy as to whether holography can serve as a good model for certain aspects of brain function. The roots of this controversy are often to be found in misunderstandings of what holography is and what the proponents of a holographic hypothesis are claiming. Furthermore, a feature model is often seen as a more viable alternative.

Holography was invented in 1949 by Dennis Gabor, a mathematician. Primarily, holography is a set of mathematical propositions based on modifications of the Fourier theorem. In short, the holographic hypothesis of brain function proposes a mathematical model. Criticisms levied against the hypothesis that rely on optical holography as an analogy are misguided.

The Fourier theorem states that any pattern can be analyzed into components, each of which is represented by a regular waveform of specified amplitude and frequency. In holography, the phase relations among waveforms are also critical since the waveforms become distributed over the entire surface of the recording medium. With distribution all the information encoded in the hologram is enfolded into each portion.

An initial general criticism of the holographic hypothesis of brain function concerns the Fourier transform. There is no evidence either from experiments in psychophysics or neurophysiology that input to the senses is analyzed into Fourier components that become distributed over the entire surface of the brain. Gabor was aware of this and developed what is now known as the Gabor function. This function places gaussian envelopes over the Fourier waveforms, thus constraining their otherwise infinite extent. Holograms made of patches

of Gabor functions have all the essential attributes of more globally transformed Fourier holograms.

The second general criticism of the holographic hypothesis of brain function devolves on the use of waveform representations in the model. Much of this criticism comes from investigators in the field of artificial intelligence who use digital computers to model brain and psychological processes. In the brain, however, most computations are performed by interactions among graded electrotonic electrochemical potentials, often with the aid of local circuit neurons, most of which do not possess the axon hillocks and axons in which digital nerve impulses are generated and propagated. Whether one wishes to model these local graded interactions in wave mechanical or in statistical terms such as vectors or lattices, matrices or Lie groups, is a matter of taste. The mathematics may turn out to be equivalent with regard to the operations of the neural substrate.

The advantage of a Fourier-based waveform approach is that it is essentially linear and invertible. Thus holographic image processing allows easy access to the original form of the images being processed. The advantage of the holographic stage of processing is computational power, especially correlation, and readily retrievable storage. Thus the wave mechanical model is worth pursuing. What is the evidence for it?

The neuroscience community has become more and more aware of the importance of electrotonic processing of signals in these input systems through the work of G. Bishop, K. Pribram, W. Rall, W. Freeman, G. Shepherd, P. Rakić, and

F. Schmitt. Observations that early stages of retinal processing (as well as those in most other receptor systems) are devoid of nerve impulses have provided convincing evidence of the critical role of graded potential interactions in sensory signal processing. Additionally, these observations have provided minimodels of some aspects of the functional organization of more central stations (especially of the cortical sheets that so closely resemble the layered retinal mosaic). The question that arises is whether the transfer functions that are being meticulously described for each stage of electrotonic input processing can together account for the image processing.

Two major views have emerged: That of D. Hubel and T. Wiesel emphasizes the convergence of signals onto neurons that, at successive levels of processing, progressively extract the features encoded in the signals. The other, represented in the work of F. Campbell and D. Pollen, among others, emphasizes a more parallel process that by virtue of lateral inhibition (a graded potential, electrotonic mechanism) functions linearly to encode signals in the frequency domain. In the auditory mode, the idea that the sensory system may function as a frequency analyzer goes back to the work of Ohm and Helmholtz over a century ago. In 1967 von Békésy demonstrated with an elegant series of experiments that somatosensory (and perhaps gustatory, as well) experience is processed according to more or less identical rules. What is new are the experimental results in our laboratory that indicate that neurons in the somatomotor cortex respond to limited bandwidths of the frequency of movement of a foreleg and that visual patterns are similarly processed by a mechanism sensitive to spatial frequency, the frequency of occurrence of light and dark in the input to the retina.

More recently D. Pollen and S. Ronner have demonstrated the presence in the same cortical column of cells responding to opposite phases of an input, i.e., to the sine and cosine components. H. Barlow, among others, has evidence that it is the Gabor transform that most accurately describes the transformation. R. DeValois and his group have demonstrated the anatomical distribution of frequency-tuned analyzers and have thoroughly and critically reviewed their own and others' psychophysical and neurophysiological investigations on the topic of frequency encoding in the visual system. They also have reported experiments that make implausible a Euclidian, hierarchical approach to image processing based on the detection of lines.

A more complex feature analytic process is not ruled out, however. Each cortical cell displays selectivities to several features including a limited band of spatial frequency, orientation, direction and velocity of movement, and color. Under current investigation is the nature of the output code that recognizes these features.

The two views of the sensory processing mechanism—that of a hierarchical nonlinear feature extraction process and that of a parallel processing linear frequency analyzer—are thus not mutually exclusive. Feature extraction can lead to information and frequency analysis to image processing.

A final critique of the holographic hypothesis of brain function has been that it is counterintuitive. If, however, one imagines the sensory receptor surface to be something like a piano keyboard and the topologically corresponding cortical cell assembly to function like a sounding board, a feel for the mechanism can be obtained. Input patterns to the receptors are transduced into neural frequency patterns that are transmitted to the cortical sounding board where each cell resonates to a

limited frequency bandwidth. Patterns of the complexity of sonatas can be processed in this manner.

Similarly, the counterintuitive aspects of holography can be grasped by analogy to the patterns of radio and television programs simultaneously present in the broadcast space. Each program is in fact broadcast, i.e., distributed, cast broadly over that space, and each portion of space has enfolded in it all the programs that are being transmitted at that moment. In order to make sense of any of the programs transmitted in a frequency code, we must tune in selected bandwidths that act as carriers for particular programs and retransform them into auditory and visual images. In order to make sense of the neural holographic process, the sense organs must tune in on selected bandwidths of environmental energy patterns and retransform them into images, perhaps by virtue of the motor processes of the brain.

The neural holographic model has become refined in applications to understanding memory as well as perception. Here, two forms of the model were initially pitted against one another: a matrix versus a convolutional approach. In the matrix model remembering is triggered when successive inputs are related to one another by taking the outer products of vectors representing features; while in the convolutional model correlations are achieved by superposition and by taking the inner products of these vectors.

Matrix models such as those of James Anderson have been shown to be superior in explaining categorical memory; convolutional models in explaining serial position memory effects. Pribram has shown that receptive fields in the lateral geniculate nucleus and the visual cortex can be altered (probably by influencing lateral inhibition) by electrical stimulations of the posterior and frontal "association" cortex (and the subjacent basal ganglia). Posterior stimulation enhances inhibitory surrounds thus producing a separation of excitatory centers. Such separate receptive fields are best represented by a matrix model. Frontal stimulation disinhibits with the result that excitatory receptive fields tend to merge into a more continuous processing mode which is best represented by a convolutional model. Further, the systems of the posterior cerebral convexity have been shown important to categorizing; the frontolimbic systems, to serial position (temporal tagging, parsing).

The holographic model has thus received support from neuropsychological evidence which is consonant with the evidence obtained in experimental psychology and in neurophysiology.

See also Memory, Distributed; Vision, Frequency Analysis

Further reading

- DeValois RL, Albrecht DG, Thorell LG (1978): Spatial tuning of LGN and cortical cells in monkey visual system. In: *Spatial Contrast*, Spekrijse H, ed. Amsterdam: Monograph Series. Royal Netherlands Academy of Sciences
- Marcelja S (1980): Mathematical description of the responses of simple cortical cells. *J Optical Soc* 70:1297-1300
- Pribram KH (1966): Some dimensions of remembering: Steps toward a neuropsychological model of memory. In: *Macromolecules and Behavior*, Gaito J, ed. New York: Academic Press, pp 165-187
- Pribram KH, Lassonde MC, Pito M (1981): Classification of receptive field properties. *Brain Res* 43:119-130
- Pribram KH, Sharafat A, Beekman GJ (1984): Frequency encoding in motor systems. In: *Human Motor Action: Bernstein Revisited*, Whiting HTA, ed. Amsterdam: Elsevier, pp 131-156
- Schmitt FO, Dev P, Smith BH (1976): Electronic processing of information by brain cells. *Science* 193:114-120