Nonlocality and Localization in the Primate Forebrain

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The Issues

The fact that items in memory (engrams) become to some extent distributed in brain systems (see, e.g., Lashley, 1950), has let to a search for mechanisms that mediate distribution. Among such mechanisms, the holographic hypothesis of brain function (Pribram, 1966, 1969a, 1971; Pribram, Nuwer & Baron, 1974) in memory and perception has stirred a considerable amount of controversy (see, e.g., Arbib, 1972) which has sometimes become manifest in overweaning interest (Psychology Today, Feb., 1979; Re-vision, Summer/Fall, 1978; Omni, Oct., 1982) and at others in simply being ignored (e.g., Edelman & Mountcastle, 1978). In the brain/behavioral sciences the tendency is to latch on to a concept and try to make it do more than the evidence warrants: The thalamic theories of emotion and the all encompassing and often unspecified role of the reticular formation in emotion, motivation, thought, learning, decision making, consciousness and attention come to mind as historically interesting examples. There is good reason, therefore, to review once again what the holographic hypothesis is about, its basis, its claims and limitations, and to juxtapose this review with one that deals with the formation of localized neural programs which operate on the non-local input store. A clear statement concerning what the holographic hypothesis is not about can also be helpful.

Let us begin with this last item --- what the holographic hypothesis is not. It is not a theory or model addressed to "how the brain works" in general. It does not aim to account for all brain physiology nor all of the problems of psychology. For example, the holographic hypothesis has little to say about the orderly sequencing of behavior which is explained much more readily by recourse to models based on computer programming (see, e.g., Miller, Galanter & Pribram, 1960). Evidence for localized storage of programs is reviewed in Part II of this chapter.

Nor does the holographic hypothesis of brain function take as its primary model the optical hologram. Both the optical hologram and aspects of brain function are considered to be instantiations of Gabor's mathematical proposition that encoding the Fourier or related transforms of a display allows image reconstruction of greater resolution than that provided by encoding the image per se. An additional instantiation of this mathematics is performed when digital computers perform (by way of the Fast Fourier Transform-FFT) image reconstructions as in tomography (CT scans --- computerized tomography).

Furthermore, the holographic hypothesis of brain function does not claim to contradict the localization of neural processes within systems of the brain. As we shall see, both local and non-local neural functions depend on precisely arranged connections between brain and peripheral structures, and between brain systems. Such connections determine what is encoded in the several brain systems, a topic reviewed in Part II of this chapter. By contrast, the holographic hypothesis addresses the intrinsic connectivity within each system which determines how events become encoded. The strongest form of the holographic hypothesis is based on the Fourier transform but weaker forms admit of cascades of convolutions (see, e.g., Gabor, 1946), of averaging over Laplacians of a Gaussian distribution, and similar linear transforms.

What then does the hypothesis claim? The hypothesis claims to provide a model at the neurological level that accounts for the apparent distribution of memory storage; the vast capacity of that storage; the imaging capability of human sensory systems and some of the properties of associative recall. The hypothesis does not claim exclusivity (i.e., that other models cannot account for these phenomena) but since it can be manipulated independently of brain it can provide insights into the necessary constraints such models must embody. Such "in vitro" procedures are successfully applied in other sciences (e.g., biochemistry, where reactions can be examined in test tubes apart from the biological context in which they occur).

Finally, although the mathematical expressions (forms of orthogonal polynomials) that describe the theory are known as spread functions and their optical realization in photography can result in a boundariless distribution of information on film, these global transforms are not the only form of holography. In radio-astronomy (e.g., Bracewell, 1965) and radar applications, as well as in constructing multiplex optical holograms, strips or patches of holographically transformed information are spliced to provide not only a three-dimensional image (as in ordinary holography) but also a moving image. As we shall see, such patch, strip or multiplex holograms, represented mathematically by Gabor and not Fourier transforms, provide models more in consonance with the brain facts than any globally distributed system. Most of the objections that have been formulated (see, e.g., Julesz & Caelli, 1979) have addressed the limitations of global Fourier transforms to deal with psychophysical data.

These don'ts and do's have characterized the model from its inception. Over the 20 years that have intervened, however, these characteristics have become articulated in more precise terms and data have accumulated in support of the model.

The first part of this paper will be concerned for the most part with these accumulations of data. Most of the data were not gathered with the model in mind. And the model itself did not originate in brain/behavior studies but from the problems posed by morphogenesis during embryological development: Structural theories based on the principle of chemical gradients and resonances that "tune" specific locations in cytoplasm as inductors for organelles have been influential in embryology since before the turn of the century (see, e.g., Jacques Loeb, 1907, and Paul Weiss, 1939). In 1906, Goldscheider suggested that the structures of perception and memory might be similarly constructed by resonances among wave fronts created by sensory inputs in brain, especially cortical, tissue. In 1942, Lashley adopted this view as an alternative both to Köhler's field (as stated in final form in 1958) and to a localizationist view in which one percept or engram, one feature of experience, is matched to one neuron or neuron assembly. Lashley was never satisfied with this adoption because he could not envision the specific mechanisms which would give rise to resonant (and interfering) wave fronts in brain tissue and, equally important, how these, in turn, might be responsible for the structures that comprise perception and engram. He nonetheless held to the view that neither field nor localization (as, e.g., in the sophisticated development by Hebb, 1949) could account for the complex relationship between brain anatomy and phenomenal experience or deal adequately with the encoding of memory.

The holographic hypothesis provides specific mechanisms which can give rise to resonant (and interfering) wave fronts (which can as well be viewed in statistical terms as composed of vectors in matrices or latices of neural events in brain tissue) and demonstrates how these in turn might be responsible for the images that comprise perception and the distributed engrams that make up the memory store. In order to fully display the utility of the model, it will be contrasted with two other major classes of proposals, field theory and feature correspondence theory, which until very recently provided the only major alternative classes of models. Field theory is shown wanting with respect to perception although it plays an important role in learning. The chapter then procedes to apply the results of research on feature correspondence and holographic encoding to object perception, which is found to depend on the interaction of the sensory with the motor mechanisms of the brain. Part II procedes to detail the operations of further stages of motor-like programming to constitute the cognitive operations embedded in various techniques of learning and memory encoding.

PART 1: FIELDS, FEATURES AND NEURAL HOLOGRAPHY

In the introduction it was noted that until the immediate present there really have been only three classes of neural mechanisms proposed to explain the properties of perception. The three may, for convenience, be labeled field theoretic, feature correspondent, and holographic.

Wolfgang Köhler proposed that direct current (D.C.) fields were set up in the brain cortex by sensory stimulation and that these fields were isomorphic with, i.e., had the same shape as, the phenomenally perceived stimulus. Köhler and Wegener (1955) showed that in fact sensory stimulation did result in D.C. shifts and in our laboratory we showed that such shifts were accompanied by desynchronization of the electrocorticogram (Gumnit, 1960).

However, several experiments which throw doubt on the relationship between such shifts and perceptual performance were performed by Lashley, by Sperry, and by Pribram. In these experiments gold foil was placed over the surface of the cortex (Lashley, Chow & Semmes, 1951); mica strips were implanted in cross-hatched cortex (Sperry, Miner & Myers, 1955), and aluminum hydroxide cream injected in minute amounts into the cortex to produce gross abnormalties (Pribram, 1951; Kraft, Obrist & Pribram, 1960; Stamm & Knight, 1963).

Figures 1 and 2 about here

In none of these experiments did the animals show any change in their ability to discriminate among cues --- gross alteration of the cortical D.C. field was not accompanied by any gross change in perceptual performance. These findings take additional meaning from the fact that the aluminum hydroxide cream implantation produced a five-fold retardation of learning and that imposing direct currents across cortex impairs (when cathodal) and enhances (when anodal from surface to depth) learning (Stamm & Rosen, 1972). Direct current fields are thus shown capable of biasing learning rate; and at the same time such fields seem to be unrelated to the structuring of percepts. We turn therefore to the evidence for feature correspondence and holographic encoding for explanations of the neural mechanisms responsible for perceptual phenomena.

Feature Correspondence Theory

Definition

Field theory and feature correspondence concepts either explicitly or implicity imply a brain-perceptual isomorphism. In the case of feature correspondence isomorphism is thought to be established when a particular cell or cell assembly responds uniquely to a feature of the phenomenally experienced image --- i.e., a feature of the imaged object is detected. It is then assumed that the organism's response to the total object is composed by convergence of the outputs from a set of feature selective elements onto a higher level neuroperceptual unit -- a "pontifical" cell or cell assembly composed of like elements ("cardinal" cells).

In the late 1950's and early 1960's Hubel and Wiesel (e.g., 1959) discovered that the center-surround organization of the dendritic microstructure of cells (their receptive fields) in the peripheral visual system became elongated. Further, they presented indirect evidence that this elongation might be due to convergence onto the cortical cells of fibers from cells with center-surround receptive fields. Their demonstration emphasized that cells in the visual cortex responded best to bars of light presented in specific orientations. It was easy to generalize these findings into a Euclidian geometry of brain function: points to oriented lines, to curves and planes, to complex figures of all sorts. The search for feature detectors was on.

The results of the search were by no means meager. For instance, one cell in monkey cortex was found to respon maximally to a monkey's hand (Gross, Bender & Rocha-Miranda, 1969); another cell was shown to respond best when a stimulus was repeated six times (Groves & Thompson, 1970); still others appeared to be activated largely by vocalizations of their own species (Maurus & Ploog, 1971).

Features Extracted From Noise

There is a considerable body of evidence which supports the conception that at least some of the feature properties matrix are inborn (see, e.g., Wiesel & Hubel, 1965a, 1965b; Chow, 1961, 1970; Ganz, 1971). True, these properties must be exercised in an ordinarily rich environment lest they deteriorate and/or develop abnormally (Wiesel & Hubel, 1965a, 1965b; Pettigrew, 1974). And there is some additional tuning that can occur as a result of specialized environmental inputs (Hirsch & Spinelli, 1970; Blakemore, 1974). In the context of phenomenal perception, these data can be taken to indicate that a feature matrix is a relatively stable property of the organism's sensory (receptor to cortical) system. Tuning of elements in that matrix by sensory input from the environment is feasible, but the elements to be tuned are characteristic of the organism.

An additional experimental result bears on this issue: Sutter (1976), in my laboratory, identified a cortical unit with simple receptive field properties and then stimulated it with visual white noise, created by a random presentation of spots on a TV monitor. The experiment was undertaken to determine whether the response of the cell was linear (i.e., whether all of the variance could be accounted for by the first kernel of a Wiener polynomial). Much to our surprise, within the first 30 milliseconds the cell responded only to those spots within its receptive field, exactly as it does to the conventional mapping procedure using a lines in particular orientations. Ten milliseconds later an inhibitory flank appeared, as would be predicted for simple receptive field properties from intracellular recordings (Creutzfeldt, Kuhnt & Benevento, 1974). In effect, the cell extracted the features "elongation" and "orientation" from noise on the basis of its own propensities. Similar results were obtained for frequency selection in the auditory system (Hosford, 1977). Clearly, the cells are _selecting_ from the multiform sensory input only those properties to which they are sensitive.

Figures 3 and 4 about here

The Conjoining of Features by Single Neurons

The specific selectivities of neurones can be misleading, however, if they are interpeted as showing that the cells in question function as feature detectors. To serve as a detector, the output of the cell must uniquely reflect the input feature and this is only occasionally the case. More often a cell responds to a variety of feature triggers. In the visual system, for example, a cell which responds selectively to lines in a specific orientation, will modify that response with a change in luminance, with the direction of movement of those lines and the velocity of such movement (Spinelli, Pribram & Bridgeman, 1970; Pribram, Lassonde & Ptito, 1981). Futhermore, that very same cell may show a different response to color and even be tuned to a specific auditory frequency (Spinelli, Starr & Barrett, 1968). Finally, the number of lines, their widths and spacings, also influence the response of the cell which suggests that "stripes" rather than "lines" form the critical stimulus dimension for their orientation selectivity (DeValois, Albrecht & Thorell, 1979; Glezer, Ivanoff & Tscherbach, 1973; Movshon, Thompson & Tolhurst, 1978a,b,c; Pollen & Taylor, 1974; Schiller, Finlay & Volman, 1976). More of this in a moment.

Findings such as these, and they are equally true of other systems (see, e.g., Evans, 1966), for cells in the auditory cortex) make untenable the view that these cortical cells are simple detectors of features. Nonetheless, each cell is selectively responsive to variety of highly specific stimulus dimensions, the "feature triggers." Some of these dimensions appear to be mapped into recognizable patterns in adjacent cells --- e.g., orientation selectivity has been related to the columnar structure of cortex (Hubel & Wiesel, 1977) and selectivity to line width and spacing has been reported to be a function of cortical layers (Maffei & Fiorentini, 1973). Other stimulus dimensions such as the tuning of cells in the visual cortex to auditory frequencies are distributed without any apparent regularity over much wider expanses of cortex. These distributed forms of organization become especially evident when recordings are made from groups of neurons when problem solving is being investigated (John, Bartlett, Shimokochi & Kleinman, 1973; Gross et al., 1979; Pribram, Spinelli & Kamback, 1967).

The view obtained from the results of these studies is that, rather than feature detection by single neurons, some sort of feature selection is effected by neuron networks. For example, at the time Hubel and Wiesel discovered the orientation selectivity of receptive fields of cells in the visual cortex (1959) they also described additional properties called simple, complex, and hypercomplex by which various receptive fields could be distinguished. (The simple property is characterized by an elongated excitatory band flanked by one or more inhibitory sidebands; the complex property by a more homogenous excitatory field; the hypercomplex property by end-stopping of the excitatory band by inhibition.) These discoveries have led to the almost universal interpretation that the neurons of the visual cortex can be classified according to their receptive field properties.

Based on this seminal work of Hubel and Wiesel in the late 1950's, which assigned cells to categories such as concentric, simple, complex, and hypercomplex (1959, 1962), a series of studies were begun in our laboratory during the mid 1960's (Spinelli & Barrett, 1969; Spinelli, et al., 1970; Phelps, 1973, 1974). We attempted to make a quantitative assessment of the nature of the properties defining these categories by using a computer controlled experimental situation in which single, double, and multiple spots and lines were drifted across the visual field of cats and monkeys. In this way the receptive field of a cell could be accurately mapped because the computer "knew" where the spots or lines were located and could assign the response of the unit to that location in a set of bins that represented the possible locations in which the spot(s) or line(s) might appear. In addition, elementary sensitivities of the cells to such stimuli as color, and the direction and velocity of movement were assessed.

The most striking result of these and subsequent experiments (Pribram et al., 1981) was the fact that each cell in the primary visual projection cortex has multiple selectivities and that the cells differed in the combinations of these selectivities. Thus it became impossible to classify the cells --- only the properties of a network of receptive fields were amenable to specification and classification. These properties were to a large extent, though not exclusively, characterized by the elementary stimuli that were used to study the receptive field network. In short, each neuron in the primary visual cortex has already conjoined elementary sensory properties in some characteristic combination.

Here are some examples: G. H. Henry (1977) has noted, in several thousand explorations, hypercomplex properties (i.e., an inhibition when elongation of the structure extends beyond certain limits) were found only rarely and that when present, the receptive field also showed either complex (i.e., responsive to such a stimulus anywhere in its receptive field) or simple (i.e., showing excitatory and inhibitory regions within its receptive field) properties. Schiller, Finlay, and Volman (1976) found so many properties for each neuron they examined that they attempted classification via a multidimensional statistical analysis. Though not undertaken by them, Henry's and Schiller's approach, drawn to its logical conclusion results in a classification of receptive field (i.e., network) properties not a classification of single neurons (Pribram et al., 1981).

Thus any conceptualization based on the idea that sensory feature elements are kept isolated in the primary visual projection systems is wrong. Whatever the nature of feature analysis and of channel separation, it is not due to a limited line, neuron to neuron mechanism.

Let me repeat this point once again for it is critical to any understanding of the issue of whether perception is constructed by conjoining features which are inithe cell. Some of these cells in the visual cortex are even selectively tuned to acoustic frequencies (Spinelli, Starr & Barrett, 1968) and groups of neurons and even single cells show late responses (300--400 msec after a stimulus is presented) only to a rewarded cue in a problem solving situation (Pribram et al., 1967; Bridgeman, 1982).

This conjoining of properties in a receptive field of a neuron does not mean however that each neuron represents those conjunctions which characterize any particular object. No pontifical "grandfather" or "grandmother" cell has been found whose output is uniquely specified by an object. It remains possible that such specificity becomes encoded in the pattern of the output of a neuron --- a pattern which can be specified by an interresponse interval histogram or burst profile. But to date this has not been accomplished.

How then can we account for the perception of objects and events? Most likely, the perception of objects and events must be constructed by addressing a population of neurons whose response forms a spatial pattern unique to that feature. According to this formulation the population of neurons responds to a feature much as does an audience when asked: all those who are blond please raise your hand. Now all those wearing red sweaters raise your hand. And now those who are female raise yours. Each query elicits a distinct pattern which simultaneously selects a unique pattern from a pool of properties in which these properties are already to some extent haphazardly conjoined. The next stage of processing thus involves the recognition of spatial pattern which is dependent on the precise anatomical connectivity between the primary sensory receiving cortex (the striate, for vision) and its perisensory (the prestriate) surround.

Feature selection by neural networks can be considered to be a form of feature correspondence. As noted in the paragraphs above, however, the nature of the features responded to by a neural network response pattern is considerably different from their perceived phenomenal nature. The spatial pattern made by neurons which respond to a feature though unique to that feature, do not resemble the feature in any way. Feature correspondence must be viewed, therefore, as non-isomorphic, i.e., there is no geometric correspondence between phenomenal experience and the neural patterns to which that experience corresponds. Given this caveat, the evidence for feature correspondence is substantial. Unique neural response patterns can be abstracted from the multiple conjoined selectivities of neurons and neuron assemblies. The question remains as to how this abstraction is accomplished.

Object Perception and the Motor Systems of the Brain

It is the importance of movement to perception that provides the key to an answer to the second question posed earlier: How does the selection/conjunction process proceed to emphasize some features to the exclusion of others? Try the following demonstration. Have someone touch you with a pencil or other object. You feel the touching, rubbing, pressure, etc. These are elementary qualities of tactile sensibility. Now grasp and rotate the same object in your palm by active manipulation. Suddenly an object (a pencil) has materialized!

There is an intermediate perception that can be achieved when the passive touching is performed in a reasonably regular fashion. Thus and X or a T may be identified as a pattern --- somewhat intermediate between a passive sensation and an object. Auditory perceptions are based on the relative frequencies of vibratory stimuli --- movement in time is involved. It is likely that a similar mechanism operates in vision. Here the mechanism is based on relationships among spatial frequencies, one of the feature properties of the receptive field matrix of the visual cortex (Campbell, Cooper & Enroth-Cugell, 1969; Campbell & Robson, 1968; DeValois et al., 1979; Glezer et al., 1973; Maffei & Fiorentini, 1973; Movshon et al., 1978a,b,c; Pollen & Taylor, 1974; Pribram et al., 1981; Schiller et al., 1976). Movement is provided by the constant tremor-like displacements of the eyeball. When an image is artificially stabilized on the retina, pattern vision ceases within seconds (Ditchborn & Ginsborg, 1952; Riggs, Ratliff, Cornsweet & Cornsweet, 1953; Heckenmueller, 1968).

How are such stable spatial patterns generated in the cortex? Recall that direction of movement and orientation as well as frequency characterize the spatial properties of the receptive field network. These properties can combine into geometric (Fourier) descriptors which designate contours of patterns. Schwartz, Desimone, Albright, and Gross (1983) have analyzed the spatial frequency spectra at many orientations of a stimulus (Fourier descriptors are derived from response of neurons to spatial frequency at each orientation of a stimulus) of receptive fields in the inferotemporal cortex and decoded them in terms of Fourier descriptors: a variety of stick figure contours emerge. The inferotemporal cortex does more than develop contours as we shall see below, but contours are a prerequisit to its function in object discrimination and choice. Where contours are developed is at present unknown, although some preliminary evidence suggests that the prestriate cortex is critically involved.

Pattern perception based on contours is not identical with object perception however. The characteristic which identifies the perception of objects is constancy across changes in the sensory patterns they elicit. Constancy is achieved by a connectivity which allows the variety of images and their contours to be correlated so that only invariences remain. The averaging procedure used in analyzing event related brain electrical potentials is an example which extracts constancies from noise. Edelman and Mountcastle (1978) have detailed a model of connectivities which achieve constancies by eliminating irrelevant information. Mathematically such "degenerative" procedures are non-linear and irreversible.

An important question for research is whether such non-linearities are introduced at the object level of processing. Constancies can be developed when the functions of motor programs are initiated in systems interwoven with and adjacent to the sensory projections in the brain. One of the characteristics of the development of the mammalian brain is the progressive separation of motor from sensory cortex which may allow a substitution of the Edelman type of degenerative connectivity for the more locally symmetrical connectivities (Burgess, Wagner, Jennings & Barlow, 1981; Pribram, 1960) of the projection cortex per se. This is especially true in the somatic modality. But to some extent it is also true of the other senses (see Pribram, in preparation).

For instance, electrical excitation of the peristriate cortex (which surrounds the visual projection area) of monkeys produces eye movements which raises the possibility that object constancy in the visual mode is a function of this visuomotor system. This possibility is enhanced by the finding that in one experiment (Ungerleider, Ganz & Pribram, 1977) size constancy was shown to depend on this system. After extensive damage, monkeys respond exclusively to the retinal image size of an object, ignoring the contextual environmental and organismic factors responsible for constancy.

Sperry (1947), Held (1968), and Festinger, Burnham, Ono, and Bamber (1967) each have suggested that all of perception is essentially a motor process. In part this suggestion stems from the fact that neurons are sensitive to transients and movement produces transients. However, their analysis has failed to account for our inability to basically alter images of scenes --- despite occasional illusory conjunctions of features. As developed here, the motor systems are assigned a more restricted role --- that of developing object constancies. Objects are perceived as invariant when the organism actively moves about the environment --- whether with his eyes, hands or whole body.

As noted, Schwartz et al. (1983) have devised precise mathematical models which can extract geometric (e.g., Fourier) descriptors of shape (invariances) from such figure-ground perimetry. Whitman Richards and Lloyd

Kaufman (1969) have pointed out the relevance of this type of model to "center of gravity" tendencies which occur for spontaneous optic fixations onto figures in the presence of flow patterns of visual background noise (ground). They suggest that each pattern boundary:

> sets up a wave [in the cortical receptive field matrix] which is propagated at a constant velocity. The point at which all waves converge together will be the apparent position of the whirlpool [the fixation point]. For simple figures with no imagination, this position will be the center of gravity of the figure. The positions of the whirlpool for more complex figures can be calculated as outlined by Blum (1967).

They conclude by stating that they would like to consider the possibility that a "center of gravity" analysis "which regulates oculomotor activity may be occurring at the same time that the form of the pattern is analyzed. Thus, it is the flow pattern and not the form of the pattern which is the principal correlate of the fixation behavior." And I will add, the flow pattern in a natural setting is, of course, largely determined by movement. It is movement-produced flow patterns which initiate the emphases and de-emphases (conceptualized as wave fronts and vectors) which constitute selection within the feature matrix of the cortex. Note here that the direction of control is from the peristriate to the striate cortex. Control can be effected via corticofugal efferents to subcortical loci which in turn influence the geniculo-striate system, or control may be exercised directly via peristriate to striate corticocortical connections.

As in the Richards and Kaufman experiment, flow patterns can originate in the environment or, as so often occurs naturally, they are initiated by movement of the organism. Movement can consist of directional displacement or it can be oscillatory as in the spontaneously occurring eye movements which prevent the fade out which occurs when retinal images are experimentally made stationary. In either case, the peristriate cortex becomes involved in fixating the "whirlpool" of the flow patterns.

In the olfactory mode such oscillatory movements are produced by respiration. As Freeman (1981) has elegantly demonstrated, oscillatory movements create the formation of wave packets which interact in terms of their spatial frequency. Both Freeman (1981) and Grossberg (1981) have presented mathematical models of the development of perceptual constancies based on such interactions.

Nonlocality and Holonomic Theory

Definition

A likely mechanism by which the abstraction necessary to object perception is achieved lies in the powerful correlational facility of holonomic transformations, the transformations which make holography possible. The idea that the neural network performs holonomic transformations on sensory input must be clearly distinguished from both field theories and feature correspondence theories. In a holonomic transformation the various stimulus dimensions become enfolded into every part of the transform domain --- a set of neural signals is transformed and transfer functions, readily dealt with either by wave form or statistical mathematics describe the transformation. This duality makes holonomic theory akin to quantum mechanics, where the dual nature of quanta of electromagnetic phenomena being described. This a combination of wave form and statistical approaches has been found to be most powerful (see, e.g., Julesz, 1971, for the visual system and Flanagan, 1972, for the auditory system). Transformation of a set of signals into an enfolded order is very different from simply generating a D.C. field in cortex by the arrival of neural signals. Holonomic theory, a quantum theory, is therefore not a field theory although it is related to field theory in that wave mechanical descriptions are relevant and the fact that holistic rather than point to point analysis is emphasized.

Holonomic theory thus resembles feature correspondence theory to some extent although once again the two can be sharply distinguished. The similarity comes from the fact that performing a transform a second time will reinstate the image (with all its features) from the transform domain. The difference between holonomic transformation and feature correspondence is that the transform domain is recognized in the strongest form of the theory as <u>the</u> domain in which neural networks operate. The finding of multiple feature selectives of most brain cells and cell assemblies is compatible with such a view. As we shall see, however, this strongest form of the theory does not account for all the available data, thus necessitating some specifiable modifications. In either the strongest or modified version <u>features are generated, constructed, when the encoded transform domain is addressed</u> through additional sensory input or by "reference" from other neural processes such as sensitivities to internally produced stimulation.

There is thus no brain-perceptual isomorphism in the holonomic theory as there is in the field theories. Rather, phenomenal experience is generated when sensory or internally derived inputs activate a holographic process or store. There is therefore no necessary geometrical identity between neural response patterns and phenomenal experience, just as in an optical hologram there is no identity between the patterns of silver grains on the photographic film and the image produced when that film is properly illuminated. Even a functional identity between phenomenal experience and brain processes becomes suspect if this means ignoring the input to senses from the world outside the organism and the input to other receptors from within the body.

The Neural Microstructure

A fundamental observation concerning the structure and function of the nervous system is the fact that the relationship between locations that characterize peripheral receptors and effectors is reflected in the organization of the input to and output from the brain cortex. The peripheral relationship may become distorted through convergence in the pathways to synaptic way stations that are intercalated between periphery and cortex and by divergence from those way stations --- but enough of the relationship is maintained to be recognizable as a mapping of periphery onto cortex. In order for such cortical mapping to be possible, signals must be transmitted from and to specific locations in the periphery by way of pathways of nerve axon systems in which impulses are generated and propogated.

A second fundamental fact about the organization of the nervous system is that these peripheral-cortical axonal pathways are interlaced at every station, i.e., in the periphery (as for example at the retina), and at the cortex (as for example in the striate cortex), with cells which possess either very short fine-fibered axons or no axons at all. Such cells, called local circuit neurons (Rakic, 1976) are incapable of maintaining and transmitting action potentials, the nerve impulses, which convey signals over distances. Instead, these local circuit neurons are characterized by profusely branching dendrites which intersect with others from adjacent neurons. The electrical potential changes in such dendritic structures tend to be graded rather than impulsive and when impulses are generated they are small in amplitude, decay rapidly and thus are not conducted over any considerable distance (Rall, 1970; Shepherd, 1974). In sum, the potential changes in these dendritic arborizations are most often hyperpolarizing and thus inhibitory (e.g., Benevento, Creutzfeldt & Kuhnt, 1972).

The interaction between vertical (i.e., periphery to cortex) axonal transmission pathways and the interlaced horizontal dendritic networks has been worked out in several sensory systems by extra-cellular recordings made from the separate neurons composing the axonal transmission pathways. In essence, the interaction leads to a center-surround organization when a discrete stimulus excites the neuron. A center-surround organization is one in which the spatial extent of the signals transmitted becomes enveloped in a penumbra of signals of opposite sign. This center-surround organization often displays the characteristics of a wave form in that several excitatory and inhibitory bands surround the center, much as ripples are formed in a pond when the surface is excited by a pebble. Precise mathematical descriptions of such center-surround organizations have been given by Bekesy for the auditory and somatosensory systems (1959), and by Hartline (1940) and by Rodieck and Stone (1965) for the visual system (see also the review of early formulations by Ratliff, 1961). The data obtained from the olfactory system appears somewhat more complicated (Shepherd, 1974), but mathematical treatment has been successfully achieved by Freeman (1975).

The results of these studies have in common the finding that whatever the nature of the inciting stimulus to receptor excitation, such excitation and its subsequent processing can be readily formulated in terms of a calculus describing the microstructure of a network of hyper- and depolarizations. This formulation shows that the principle of superposition applies to the local spatial interactions between excitation (depolarizations) and inhibition (hyperpolarizations). Superposition indicates that the system is linear within the ranges examined and that a wave form interpretation of the data is useful. This does not necessarily mean that the dendritic potentials actually make up discernable wave fronts --- what it does mean, at the minimum, is that the center-surround data describe transfer functions by which a matrix of discrete polarizations is related to an exciting input, functions which can readily be treated by linear wave equations.

Holography

These mathematical treatments of the data obtained from recordings of potentials of single neurons in the nervous system are akin to those which spawned holography. In 1946 Dennis Gabor devised a mathematics which showed that image reconstruction might attain greater resolution if, instead of intensity, the pattern of wave fronts generated on a photographic film by an exciting electron or photon were recorded. Gabor addressed his mathematics to electron microscopy but in the early 1960's optical holography succeeded in implementing this image processing technique in such a way that the properties of holograms became readily demonstrated (Leith & Upatnicks, 1965). The essential properties are: 1) the holographic store is distributed; 2) vast amounts of storage can be concentrated in a small holographic space; 3) image reconstruction is three-dimensional, displaying constancies and parallax, and is highly textured; 4) images do not appear coextensive with the holographic store; they are projected away from the film surface; 5) the hologram has associative properties; when it is made by the reflected light of two objects, subsequent illumination of the stored hologram by light reflected from only one object will reconstruct a "ghost" image of the missing object.

These properties of holograms are so similar to the elusive properties that neuroscientists and psychologists (see, e.g., Boring, 1942) sought in brain tissue to explain perceptual imaging and engram encodings that the holographic process must be seriously considered as an explanatory device. In doing this, the caution must, however, constantly be exercised that it is the mathematics of holography and brain function that needs to be compared and tested, not the optical holograms or computer instantiations of holography.

The essentials of this mathematics can best be summarized by reference to a particular form of holography --- the construction of a Fourier hologram. The Fourier theorem states that any pattern, no matter how complex, can be decomposed into a set of component, completely regular, "sine" waves. The Fourier transform of an image is formed by encoding these component wave forms. Thus, in the transformed record each point indicates the presence of a particular component wave form rather than the corresponding local intensity as in an ordinary record. Take for comparison an ordinary photograph and a Fourier transformed record. The ordinary photograph is made up of a mosaic of points of varying intensities, the intensity of each point corresponding to the intensity of a point of light reflected from a specific location on the object being photographed. In the Fourier transformed record, by contrast, each point represents the amount of energy present in a wave form component of the entire array of light reflected from the object. The bandwidth of that component may vary; the resolving power of the transform is in part dependent on this bandwidth.

To make a (Fourier) hologram, two such Fourier transformed records must be linearly superposed. Mathematically, this is performed by the transfer function in which one record is convolved with the other and storing the resultant complex conjugate. In essence, convolving consists of "multiplying" the wave forms together. Now each point in the record contains this "multiplication," i.e., the resultant of superposing the energy contained in two wave form components derived from the entire array of reflected light. A holographic record can be made by superposing the Fourier transform of the light reflected from two (or more) objects or by using the transform of a non-reflected reference. When two or more objects are used, the light reflected from each serves as a reference for the other(s). This accounts for the property of associative recall noted above. In addition, since parts of objects as well as whole objects serve as sources of reflection and thus as references for other parts, constancies are generated when images are (re)constructed. Constancies are therefore the result of the fact that the transformed "view" of any part of the objects acts as a reference for every other part.

It is these enfolding properties of holograms that make them so counterintuitive. Within the holographic domain geometry as we sense it disappears and is replaced by an order in which the whole becomes enfolded and distributed into every part, thus the term hologram. But from each part the whole can again be reconstituted. This is due to another property of the Fourier theorem: applying the identical transform inverts the wave form domain back into the image! The process (the Fourier transform function) that converts images into wave forms can therefore also accomplish the inverse and convert wave forms into the images.

This parsimony in processing raises the question of utility. If image and wave form domain are so readily transformed into each other, why bother? The answer to this question is that correlations are much simpler to accomplish in the wave form domain --- they essentially entail superposition, multiplication. That is why the Fast Fourier Transform (FFT) has proved so useful in computer programming as for instance when image reconstruction by CT scan in x-ray tomography is desired. It is this power of the Fourier domain that the brain can exploit.

The Transform Domain

What then are the transfer functions that describe the transformations of sensory and bodily inputs into a brain holographic process? And what are the limits of explanatory power of such transfer functions with respect to the data at hand? The first suggestion that brain processing might involve a Fourier analysis was made a century ago for the auditory system by Ohm, the same Ohm who formulated Ohm's law of electricity. This suggestion was adopted by Herman V. Helmholtz, who performed a series of experiments which led to the place theory of hearing --- essentially a view of the cochlea as a piano keyboard whose keys, when struck by acoustic waves, would initiate nerve impulses to the brain where resonant neurons were activated. This view was modified in this century by George von Bekesy (1959), whose experiments showed the cochlea and peripheral neurosensory mechanism to operate more like a stringed instrument sensitive to superposition of acoustic wave forms. Good evidence has accrued to the effect that a major effect of initial auditory processing can be described in terms of a time-limited Fourier transform (i.e., a Gabor-like) of the acoustic input (Evans, 1974).

Bekesy then went on to make a large-scale model of the cochlea composed of a set of five vibrators set in a row (1959). The model could be placed on the forearm and the phase of the vibrators adjusted. At particular adjustments the phenomenal perception produced by the model was that of a point source of stimulation. When two such model "cochleas" were properly adjusted and applied, one to each forearm, the point source appeared at first to jump alternately from one forearm to the other, and then suddenly stabilize in the space just forward and between the two arms. In short, the stimulus was "projected" away from the stimulating source and receptive surface into the external world.

Both macro- and microelectrode studies have shown that multiple vibratory stimulations of the skin also evoke unitary responses in cortex (Dewson, 1964; Lynch, 1971). The electrical potentials do not reflect the actual physical dimensions of the stimulus. Instead, they indicate that the sensory process has transformed the physical stimulus according to some transfer functions. Bekesy noted that sensory inhibition, effected by lateral inhibitory dendritic networks of neurons, is the responsible agent in the transformations.

Evidence is therefore at hand to indicate that the input to the ear and skin becomes transformed into neural patterns that can be described by sets of convolutional integrals of the type that Gabor (1969) has suggested as stages in achieving a fully developed holographic process. In the visual system as well, such transformations have been described by Rodieck (1965) as convolving input with retinal receptive field properties as recorded from units in the optic nerve.

Figure 5 about here

The manner in which such a stepwise process occurs is best worked out for the visual system. A second step in the process occurs at the lateral geniculate nucleus where each geniculate cell acts as a peephole "viewing" a part of the retinal mosaic. This is due to the fact the each geniculate cell has converging upon it some 10,000 optic nerve fibers originating in the ganglion cells of the retina. The receptive field of the geniculate neuron is composed of a center surrounded by concentric rings, each consecutive ring of sharply diminishing intensity and of sign opposite to that of its neighbors (Hammond, 1972). This type of organization is characteristic of units composing a near field Fresnel hologram (Pribram et al., 1974).

Figures 6 and 7 about here

At the cortex the transformation into a Fourier-like domain becomes complete. As noted in the section on feature analysis, Campbell and Robson (1968), Pollen, Lee, and Taylor (1971), Maffei and Fiorentini (1973), and Glezer et al. (1973) began to use gratings as stimuli (e.g., Schiller et al., 1976; Pribram et al. 1981). These studies have repeatedly confirmed that the cells in visual cortex are selectively tuned to a limited band- width of spatial frequency of approximately an octave (1/2 to 1-1/2 octaves). The spatial frequency (or wave number) of a grating reflects the width and spacings of the bars making up the grating. When such widths and spacings are narrow the spatial frequency is high; when widths and spacings are broad the spatial frequency is low. Ordinarily the term frequency implies a temporal dimension --- in the case of spatial frequency this temporal dimension can be evoked by sequentially scanning across the grating. (The temporal effect is most dramatic if an object is moved across the light path of a projected grating.) Conversion to a temporal dimension is, however, not necessary. The grating is a filter whose characteristics can be expressed either as spatial or temporal or both.

Figures 8 and 9 about here

The difference between a feature correspondence and a holographic transform approach has recently been brought into sharp focus by tests of hypothesis devised to contrast the two. In the visual cortex the center-surround organization of visual receptive fields that obtains in the geniculate nucleus gives way to an elongated receptive field with side-bands of the opposite sign. Hubel and Wiesel in their original discovery of this change (1959) emphasized that lines presented at specific orientations were most effective stimuli to activate units with such receptive fields. They also presented evidence that elongated fields might be composed by convergence from geniculate cells with spot-like concentric fields. The feature-hierarchy Euclidian view of feature correspondence grew naturally from these early results and their interpretation. More recently it has been shown, as noted above, that these cells with orientation selective elongated receptive fields also vary their output with changes in luminance, movement of lines across the receptive field, the direction of that movement, its velocity and the number and spacings of such lines (gratings of various spatial frequencies). In addition, it has been shown that changes in the width of single lines have little effect on the responses of these cells (Henry & Bishop, 1971; DeValois & DeValois, 1980).

Finally, in direct confrontation of feature correspondence theory, DeValois et al. (1979) showed that the complex stimulus such as a plaid or checkerboard had to be rotated in such a way that the axes of the Fourier transform rather than the edges per se of the stimulus pattern would engage the orientation selectivity of the cell. Every cell examined responded maximally when the plaid or checkerboard pattern was rotated to the degree and minute of visual angle predicted by Fourier (and no other) transform of the pattern as determined by computer (using the Fast Fourier Transform - FFT). The cortical cells were thus shown to respond holistically (i.e., to the Fourier transform of the entire pattern) rather than feature-by-feature. Movshon et al. (1978), in another elegant experiment, detailed the complimentarity between the spatial profile of the receptive fields of these cells and the Fourier transform of the stimulus giving rise to that profile. That cells in the visual cortex encode in a Fourier-like domain is thus an established fact.

Figure 10 about here

These findings do not, however, mean that the visual system performs a global Fourier transform on the input to the retina (see also Julesz & Caelli, 1979). The moving retina decomposes the image produced by the lens of the eye into a "mexican hat" receptive field organization which can be described as convolving retinal organization with sensory input (Rodieck, 1965). But the spread function, as such convolutions are called, does not encompass the entire retina: rather it is limited to the receptive field of a retinal ganglion cell. Similarly at the cortex, full fledged encoding in the Fourier domain is restricted to the receptive field of the cortical neuron. There the effect of lateral inhibition produces a Gaussian envelope, which limits the otherwise boundaryless Fourier Transform (Marcja, 1980; Burgess et al., 1981). The resulting transformation is called a Gabor function. This patchy organization of the transform domain (Robson, 1975) does not impair its holographic characteristics.

The technique of patching or stripping together Gabor, Fourier-like transformed images has been utilized in radioastronomy by Bracewell (1965) to cover expanses which cannot be viewed with any single telescopic exposure. The technique has been further developed by Ross (see Leith, 1976) into a multiplex hologram to produce three dimensional moving images when the inverse transform is effected. Movement is produced when the enconded strips capture slightly different images, as for instance when adjacent frames of a motion picture are used as the image base for the transformation.

In the multiplex hologram, spatial relationships among the Gabor-transformed patches or strips become important. Thus, this form of hologram is a hybrid from which movement can be derived. A simple hologram is characterized by translational <u>invariance</u>, i.e., the image that results from applying the increase transformation is essentially stationary and appears the same from different vantages except for changes in perspective (object constancy). By contrast, the hybrid multiplex form has encoded in the spatio-temporal domain as well as in the transform domain, and this has considerable advantage for moving organisms.

Suggestions have been made that the orientation selective elongated receptive fields that compose the visual cortex are arranged in Fibernaci spirals along the axes of cortical columns (Schwartz, 1977). Such an arrangement of the spatial relationships among the Gabor-transformed patches of receptive field would inhance still further the power of the transform domain in that three-dimensional movement (and therefore the resultant space-time relationship) would be readily explained.

Counterpoint

As noted, the multiplex hybrid nature of cortical holographic organization serves as a warning that any simply conceived "global-Fourier-transform-of-input-into-cortical-organization" is untenable. Futhermore, the multiple selectives of cortical cells in the visual (Spinelli et al., 1970; Spinelli et al., 1968; Morrell, 1972), auditory (e.g., Evans, 1974) and somatosensorymotor (e.g., Bach-y-Rita, 1972) projection areas clearly indicate that such cells serve as nodes in neural networks in which the Gabor transform is only one, albeit an important process. Several attempts have been made therefore to characterize more fully such cortical networks in terms of their essential properties. Thus, Longuet-Higgins (see Willshaw, Buneman & Longuet-Higgins, 1969) proposed an associative-net model and Leon Cooper (1973) has developed this model into a self-organizing distributed net whose mathematical description contains as a special case the

Fourier transform hologram. Julesz (1971), Uttal (1978), Borsellino and Poggio (1973), Poggio and Torre (1980), and, in our laboratories, Sutter (1976) have taken a more statistical stance. Thus, Uttal emphasizes spatial autocorrelation functions, while Poggio and Sutter rely on Wiener polynomial expansions. In addition, Poggio treats the dendritic potential microstructure in terms of the Volterra solution of cable equations. His carefully worked out proposal includes a stage of Fourier analysis and another in which the Laplace transform occurs.

David Marr, Tomas Poggio, and Whitman Richards (Marr, 1976a,b; Marr & Poggio, 1977; Richards, 1977; Richards & Polit, 1974) have developed a model based on repetitive convolving of Laplacians of a Gaussian distribution. E. Roy John speaks of "hyperneurons" constituted by a distributed system of graded potentials recorded from the brains of problem-solving animals. Such organizations have been described in terms of Lie groups by Hoffman (1947), vector matrices by Stuart, Takahashi, and Umezawa (1978), and tensor matrices by Finkelstein (1976) in which the tensors represent multidimensional Fourier transforms. Finally, Edelman and Mountcastle (1978) have proposed a degenerative group model, also based on an essentially random connectivity.

The commonalities and distinctions in these proposals can be summarized as problem areas that need further inquiry: 1) To what extent is the idealization warranted that the brain cortical connectivity is essentially random? This issue has been discussed earlier in this paper. In addition, the models proposed by Hoffman and by Poggio clearly opt for non-randomness, while others are neither explicitly or implicitly based on an assumption that an ideal system may consist of random connectivities. 2) To what extent can brain systems be treated with linear (and reversible) equations and to what extent must nonlinearities be introduced to explain the available data? Good evidence is at hand that the primary input and output systems (see, e.g., Granit, 1970) are essentially linear in most of their overall operations despite many local non-linearities. More of this in the next section.

PART II: LOCALIZATION OF NEURAL PROGRAMS

Decisional Operators

Overall non-linearities may be introduced into the system when decisions have to be made --- decisions involved in discriminating between inputs, in performing this rather than that action. On other hand, decisions may be reached by virtue of correlation functions --- essentially by cascades of linear filters. In either case decisional operations have been shown to be local functions of the intrinsic (association) systems of the brain (Pribram, 1954, 1958a, 1958b, 1972a, 1972b, 1974a, 1977). Decisional operators can enter the system in two ways: The decisions can be attained by serial hierarchical abstraction of the relevant variables (see, e.g., Gross, 1973; Mishkin, 1973; Weiskrantz, 1974), or they can be imposed by a parallel corticofugal process upon the sensory-motor systems (Pribram, Spinelli & Reitz, 1969; Ungerleider & Pribram, 1977; Christensen & Pribram, 1979; Pribram, 1971, 1974b). It is, of course, also possible that the hierarchical serial process operates during learning (as, e.g., suggested by Hebb, 1949) while parallel corticofugal operators determine momentary perceptions and performances. These operators are localized to one or another brain system. In any case, two major classes of such decisional operators can be distinguished: 1) a set of sensory-specific processes that involve the posterior cerebral convexity (inferotemporal cortex for vision; superior temporal for audition; anterior temporal for taste; posterior parietal for somesthesis); 2) in addition, a set of higher-order executive (i.e., context-sensitive, processes has been identified to involve the frontolimbic portions of the forebrain (see, e.g., reviews by Pribram, 1954, 1969c, 1973).

The Agnosias and the Posterior Cortical Convexity

Sensory Specificity

Between the sensory projection areas of the primate cerebral mantle lies a vast expanse of parieto-temporo-preoccipital cortex. Clinical observation has assigned disturbance of many cognitive and language functions to lesions of this expanse. Experimental psychosurgical analysis in subhuman primates of course is limited to nonverbal behavior; within this limitation, however, a set of sensory-specific agnosias (losses in the capacity to categorize cues) have been produced. Distinct regions of primate cortex have been shown to be involved in each of the modality-specific cognitive functions: anterior temporal in gustation (Bagshaw & Pribram, 1953), inferior temporal in vision (Mishkin & Pribram, 1954), midtemporal in audition (Weiskrantz & Mishkin, 1958; Dewson, Pribram & Lynch, 1969), and occipitoparietal in somesthesis (Pribram & Barry, 1956; Wilson, 1975). In each instance categories learned prior to surgical interference are lost to the subject postoperatively and great difficulty (using a "savings" criterion) in reacquisition is experienced, if task solution is possible at all.

The behavioral analysis of these sensory-specific agnosias has shown that they involve a restriction in sampling of alternatives, a true information processing deficit, a deficit in reference learning. Perhaps the easiest way to communicate this is to review the observations, thinking, and experiments that led to the present view of the function of the inferior temporal cortex in vision.

Search and Sampling Procedures

All sorts of differences in the physical dimensions of the stimulus, for example, size, are processed less well after inferiortemporal lesions (Mishkin

& Pribram 1954), but the disability is more complex than it at first appears --- as illustrated in the following story:

One day when testing my lesioned monkeys at the Yerkes Laboratories at Orange Park, Florida, I sat down to rest from the chore of carrying a monkey a considerable distance between home cage and laboratory. The monkeys, including this one, were failing miserably at visual tasks such as choosing a square rather than a circle. It was a hot, muggy, typical Florida summer afternoon and the air was swarming with gnats. My monkey reached out and caught a gnat. Without thinking I also reached for a gnat --- and missed. The monkey reached out again, caught a gnat, and put it in his mouth. I reached out --- missed! Finally the paradox of the situation forced itself on me. I took the beast back to the testing room. He was still deficient in making visual choices. However, as indicated by his ability to catch gnats, when no choice was involved his visually guided behavior appeared to be intact. On the basis of this observation the hypothesis was developed that choice was the crucial variable responsible for the deficient discrimination following inferotemporal lesions. As long as a monkey does not have to make a choice, his visual performance should remain intact.

To test this hypothesis, monkeys were trained in a Ganzfeld made of a translucent light fixture large enough so the animal could be physically inserted into it (Ettlinger, 1957). The animal could press a lever throughout the procedure but was rewarded only during the period when illumination was markedly increased for several seconds at a time. Soon response frequency became maximal during this "bright" period. Under such conditions no differences in performance were obtained between inferotemporally lesioned and control animals. The result tended to support the view that if an inferotemporally lesioned monkey did not have to make a choice he would show no deficit in behavior, since in another experiment (Mishkin & Hall, 1955) the monkeys failed to choose between differences in brightness.

In another instance (Pribram & Mishkin, 1955) we trained the monkeys on a task in which they had to choose between easily discriminable objects: an ashtray and a tobacco tin. These animals had been trained for two or three years prior to surgery and were sophisticated problem-solvers. This, plus ease of task, produced only a minimal deficit in the simultaneous choice task. When given the same cues successively the monkeys showed a deficit when compared with their controls, despite their ability to differentiate the cues in the simultaneous situation.

This result gave further support to the idea that the problem for the operated monkeys was not so much in "seeing" but in being able to <u>refer</u> in a useful or meaningful way to what had been reinforced previously. Not only the stimulus conditions but an entire range of response determinants appeared to be involved in specifying the deficit. To test this more quantitatively, I next asked whether the deficit would vary as a function of the <u>number of alternatives</u> in the situation (Pribram, 1959). It was expected that an informational measure of the deficit could be obtained, but something very different appeared when I plotted the number of errors against the number of alternatives.

Figure 11 about here

If one plots repetitive errors made before the subject finds a peanut --- that is, the number of times a monkey searches the same cue --- <u>vs</u> the number of alternatives this stage the monkeys with inferotemporal lesions were doing better than the controls! This seemed a paradox. However, as the test continued, the controls no longer made so many errors, whereas the lesioned subjects began to accumulate errors at a greater rate than shown earlier by the controls.

When a stimulus sampling model was applied to the analysis of the data, a difference in sampling was found. The monkeys with inferotemporal lesions showed a lowered sampling ratio; they sampled fewer cues during the first half of the experiment. Their defect can be characterized as a restriction on the number of alternatives searched and sampled. Their sampling competence, their competence to process information, had become impaired. The limited sampling restricted the ability to construct an extensive memory store and to reference that memory during retrieval.

Figure 12 about here

Element Learning

The multiple object task was administered in a Yerkes testing apparatus operated manually. Because administration was tedious and time consuming, and because inadverdant cueing was difficult to control, an automated testing device was developed (Pribram, Gardner, Pressman & Bagshaw, 1962; Pribram, 1969b). The resuslting computer controlled Discrimination Apparatus for Discrete Trial Analysis (DADTA) proved useful in a large number of studies, ranging from testing one-element models of learning (Blehert, 1966) to plotting Response Operator Characteristic (ROC) curves to determine whether bias was influenced toward risk or toward caution by selected brain resections (Spevack & Pribram, 1973; Pribram, Spevack, Blower & McGuinness, 1980).

To investigate whether learning proceeds by sampling one element at a time, eight monkeys were trained on a two-choice and a five-choice sample of which only one cue was rewarded. The choices of individual monkeys were plotted for each of the cues sampled. As can be seen from the accompanying figure (Fig. 13), sampling of cues is initially random, producing prolonged periods of stationarity. Then, at some point, behavior becomes concentrated on the rewarded cue in steps, each of which is preceded by another period of stationarity, and the elimination (i.e., choice drops to zero) of one of the unrewarded cues.

Figure 13 about here

The study was undertaken in order to determine whether crosshatching (with a cataract knife) of the inferior temporal cortex would produce subtle effects which would otherwise be missed. No such effects were observed. By contrast, restricted undercutting of the inferior temporal region, which severed its major input and output connections, produced the same severe effects as extensive subpial resection of the cortex per se. Sampling was severely restricted as in the multiple object experiment (Pribram, Blehert & Spinelli, 1966).

Subtle effects are obtained, however, when abnormal electrical foci are induced by implanting epileptogenic chemicals in the cortex. In such preparations the period of stationarity in a two choice task is increasd five-fold. Despite this, the slope of acquisition, once it begins, remains unaffected. Obviously during the period of stationarity something is going on in the nervous system, something which becomes disrupted by the process which produces the electrical abnormality. Perhaps that something devolves on distributing the effects of trial and error over a sufficient reach of the neural net until an adequate associative structure is attained.

Cognitions

How do the search and sampling systems interact with the perceptual and motor systems to produce skilled performance? Recovery functions in the primary visual and auditory systems are influenced by electrical stimulations of the sensory-specific intrinsic and the frontolimbic (see next section) systems (Spinelli & Pribram, 1966). This influence is a function of the attentive state of the monkey (Gerbrandt, Spinelli, & Pribram, 1970). Visual receptive fields have also been shown to become altered by such stimulation (Spinelli & Pribram, 1967). Finally, the pathways from the sensory-specific intrinsic and from frontolimbic formations (see next section) to the primary input systems have been in great part delineated (Reitz & Pribram, 1969). Perhaps the most surprising findings of these studies is that input control is to a large measure effected through the basal ganglia, structures which had hitherto been thought of as regulating motor function.

Figures 14, 15 and 16 about here

Thus the functions of the brain in cognition as we know it now are considerably different from the ones that early learning theorists thought they were working with. Most formulations of learning depended heavily on the concept of associative strength based on contiguity and number. Configural variables were relegated to perception and perceptual learning was, until the past two decades, denied or ignored. Further, the configural and sampling aspects of perceptual learning had not been teased apart.

An even more pervasive difficulty with classical learning theory was its dependence on the reflex-arc, stimulus-organism-response model of brain function. We now know that the brain is organized along servomechanism principles: The discovery of the function of the gamma efferent fibers of motor nerves made it necessary to modify conceptions of the organization of the reflex and therefore of the control of behavior. The data on input control cited above indicate that even the "highest" (the cognitive) systems of the brain exert their influence via the input to the brain rather than via its output. In fact the control over input is exercised via the same motor structures (the basal ganglia) which, when they influence motor behavior, do so by "setting" the muscle spindle receptors by means of the loop.

Feedback and feedforward loops, not unidirectional input-output arcs, are ubiquitous in central nervous system organization. Sensory functions are controlled by motor systems; behavior is regulated not by a piano keyboard control over muscle contraction but by servocontrol of the setting of muscle receptors (see Pribram, Sharafat & Beekman, 1983). Programs are constructed which organize perceptions and compose a behavioral repertoire. And these programs operate by virtue of tests, matches, and mismatches between configurations of neural patterns in memory and those produced by sensory input.

Amnesias and the Limbic Forebrain

Contextual Memory

The second major division of the cerebral mantle to which memory functions have been assigned by clinical observation lies on the medial and basal surface of the brain and extends forward to include the poles of the frontal and temporal lobes. This frontolimbic portion of the hemisphere is cytoarchitecturally diverse.

The expectation that different parts might be shown to subserve radically different functions was therefore even greater than that entertained for the more uniform posterior cortex. To some extent this expectation was not fulfilled: Lesions of the frontolimbic region, irrespective of location (dorsolateral frontal, caudate, cingulate-medial frontal, orbitofrontal, temporal polar-amygdala, and hippocampal) disrupted "delayed alternation" behavior. The alternation task demands that the subject alternate his responses between two cues (for example, between two places or between two objects) on successive trials. On any trial the correct response is dependent on the outcome of the previous response. This suggests that the critical variable which characterizes the task is its temporal organization. In turn, this leads to the supposition that the disruption of alternation behavior produced by frontolimbic lesions results from an impairment of the process by which the brain achieves its temporal organization. This supposition is only in part confirmed by further analysis: It has been necessary to impose severe restrictions on what is meant by "temporal organization" and important aspects of spatial organization are also severely imparied. For instance, <u>skills</u> are not affected by frontolimbic lesions, nor are discriminations of melodies.

Retrieval of long-held memories also is little affected. Rather, a large range of short term memory processes are involved. These clearly include tasks which demand matching from memory the spatial location of cues (as in the delayed response problem) (Anderson, Hunt, Vander Stoep & Pribram, 1976) as well as their temporal order of appearance (as in the alternation task) (Pribram, Plotkin, Anderson & Leong, 1977). A similar deficit is produced when, in choice tasks, shifts in which cue is rewarded are made over successive trials (Mishkin & Delacour, 1975). The deficit appears whenever the organism must fit the present event into a "context" of prior occurrences, and there are no cues which address this context in the situation at hand at the moment of response.

The Registration of Events as Episodes

As noted, different parts of the frontolimbic complex would, on the basis of their anatomical structure, be expected to function somewhat differently within the category of contextual memory processes. Indeed, different forms of contextual amnesia are produced by different lesions. In order to be experienced as memorable, events must be fitted to context. A series of experiments on the orienting reaction to novelty and its registration have pointed to the amygdala as an important locus in the "context-fitting" mechanism. The experiments were inspired by the results from Sokolov's laboratory (Sokolov, 1960).

Sokolov presented human subjects with a tone beep of a certain intensity and frequency, repeated at irregular intervals. Galvanic skin response (GSR), heart rate, finger and forehead plethysmograms, and electroencephalograms were recorded. Initially, these records showed the perturbations that were classified as the orienting response. After several repetitions of the tone, these perturbations diminish and finally vanish. They habituate. Originally it had been thought that habituation reflected a <u>lowered</u> sensitivity of the central nervous system to inputs. But when Sokolov <u>decreased</u> the intensity of the tone beep, leaving the other parameters unchanged, a full-blown orienting response was reestablished. Sokolov reasoned that the central nervous system could not be desensitized but that it was less responsive to <u>sameness</u>: when any <u>difference</u> occurred in the stimulus the central nervous system became <u>more</u> sensitive. He tested this idea by rehabituating his subjects and then occasionally omitting the tone beep, or reducing its duration without changing any other parameter. As predicted, his subjects now oriented to the unexpected silence.

The orienting reaction and habituation are thus sensitive measures of the process by which context is organized. We therefore initiated a series of experiments to analyze in detail the neural mechanisms involved in orientating and its habituation. This proved more difficult than we imagined. The dependent variables --- behavior, GSR, plethysmogram, and electroencephalogram --- are prone to dissociate (Koepke & Pribram, 1971). Forehead plethysmography turned out to be especially tricky, and we eventually settled on behavior, the skin conductance (GSR), heart and respiratory responses, and the electrical brain manifestations as most reliable.

The results of the first of these experiments (Schwartzbaum, Wilson & Morrissette, 1961) indicated that, under certain conditions, removal of the amygdaloid complex can enhance the persistence of locomotor activity in monkeys who would normally decrement their responses. The lesion thus produces a disturbance in the habituation of motor activity (Fig. 7).

The results of the experiments on the habituation of the GSR component of the orienting reaction (Bagshaw, Kimble & Pribram, 1965) also indicated clearly that amygdalectomy has an effect (Fig. 8). The lesion profoundly reduces GSR amplitude in situations where the GSR is a robust indicator of the orienting reaction. Concomitantly, deceleration of heartbeat, change in respiratory rhythm, and some aspects of the EEG indices of orienting also are found to be absent (Bagshaw & Benzies, 1968). As habituation of motor activity and also habituation of earflicks (Bateson, 1969) had been severely altered by these same lesions, we concluded that the autonomic indicators of orienting are in some way crucial to subsequent behavioral habituation. We identified the process indicated by the autonomic components of the orienting reaction as "registering" the novel event.

However, the registration mechanism is not limited to novelty. Extending the analysis to a classical conditioning situation (Bagshaw &

Coppock, 1968; Pribram, Reitz, McNeil & Spevack, 1979) using the GSR as a measure of conditioning, we found that normal monkeys not only condition well but produce earlier and more frequent anticipitory GSR's as time goes by. Amygdalectomized subjects fail to make such anticipatory responses. As classical conditioning of a striped muscle proceded normally, it is not the conditioning per se which is impaired. Rather, it appears that registration entails some active process akin to rehearsal --- some central mechanism aided by viscero-autonomic processes that maintains and distributes excitation over time.

Behavioral experiments support this suggestion. Amygdalectomized monkeys placed in the two-cue task described in the previous section fail to take proper account of reinforced events. This deficiency is dramatically displayed whenever punishment, that is, negative reinforcement, is used. For instance, an early observation showed that baboons with such lesions will repeatedly (day and day and week after week) put lighted matches in their mouths despite showing obvious signs of being burnt (Fulton, Pribram, Stevenson & Wall, 1949). These observations were further quantified in tasks measuring avoidance of shock (Pribram & Weiskrantz, 1957). The results of these two experiments have been confirmed in other laboratories and with other species so often that the hypothesis needed to be tested that amygdalectomy produces an altered sensitivity to pain. Bagshaw and Pribram (1968) put this hypothesis to test and showed that the amplitude of GSR to shock is not elevated as it would be were there an elevation of the pain threshold. Rather the threshold is, if anything, reduced by the ablation. This experimental result suggests that amygdalectomy produces its effremember what had happened to them for a period of time prior to the injury. The duration of such retrograde amnesia varied as a function of the severity of the injury. This suggested that the process of registering an experience in memory took some time and that the injured brain could not carry out this process. Thechemical substances immediately after they had experienced shock. The times of injection were varied in order to chart the course of the consolidation process. Once McGaugh had accomplished this he set out to locate the brain systems involved in the process. The amygdala seemed a good choice as a starting point in the search. Consolidation was now successfully manipulated by electrical and chemical stimulations much as had previously been done by peripheral chemical injections. In any such series of experiments, however, the possibility remains that all one is accomplishing by the brain stimulation is the boosting of a peripheral chemical secretion so that in essence one is doing no more than repeating the original experiments in which peripheral stimulation had been used. To control for this Martinez, working with McGaugh, removed various peripheral structures such as the adrenal gland. They found that indeed, when the adrenal medulla which secretes epinephrine and norepinephrine was absent, the amygdala stimulations had no effect (Martinez, Rigter, Jensen, Messing & Vasquez, et al., 1981).

McGaugh's experiments indicate, as had ours, that the amygdala influences the learning process via visceral and glandular peripheral processes which are largely regulated by the autonomic nervous sytem. Electrical excitation of the amygdala --- as well as of the entire anterior portion of the limbic cortex: anterior cingulate, medial and orbital frontal, anterior insula, and temporal pole --- in anesthetized monkeys and humans produces profound changes in such visceroautonomic processes as blood pressure and respiratory rate (Kaada, Pribram & Epstein, 1949). The amygdala thus serves as a focus for a mediobasal motor cortex which regulates visceroautonomic and other activities (such as head turning which is also produced by the stimulations) related to orienting.

Figure 17 about here

It appears from all this research that such peripheral activities, when they occur, can boost the consolidation process and thus facilitate the registration of experience in memory. Vinogradova (1975) has suggested that the boost given by this visceroautonomic system stands in lieu of repetition of the experience. As noted above, the experiments on conditioning suggest that visceroautonomic arousal acts somewhat like internal rehearsal. One can take visceroautonomic arousal as an indication that interest and emotions have been engaged: thus the mechanism has been tapped, which accounts for the well known fact that emotional involvement can dramatically influence learning.

Processing the Familiar

Context is not composed solely of the registration of reinforcing and reinforced events. As important are the errors, the non-reinforced aspects of a situation, especially if on previous occasions they had been reinforced. It is resection of the primate hippocampal formation (Douglas & Pribram, 1966) which produces relative insensitivity to errors, frustrative non-reward (Gray, 1975) and more generally to the familiar, non-reinforced aspects of the environment (the SΔ of operant conditioning; the negative instances of mathematical psychology).

In their first experience with a discrimination learning situation subjects with hippocampal resections show a peculiar retardation provided there are many nonrewarded alternatives in that situation: For example, in an experiment using the computer-controlled automated testing apparatus (DADTA), the subject faced 16 panels; discriminable cues were displayed on only two of these panels and only one cue is rewarded. The cues were displayed in various locations in a random fashion from trial to trial. Hippocampectomized monkeys were found to press the unlit and unrewarded panels for thousands of trials, long after their unoperated controls ceased responding to these "irrelevant" items.

It is as if in the normal subject a "ground" is established by enhancing "inattention" to all the negative instances of those patterns that do not provide a relevant "figure." This "inattention" is an active, evaluating process as indicated by the behavior shown during shaping in a discrimination reversal task, when the demand is to respond to the previously nonreinforced cue: Unsophisticated subjects often begin by pressing on various parts of their cage and the testing apparatus before they hit upon a chance response to the non-rewarded cue.

These and many similar results indicate that the hippocampal formation is part of an evaluative mechanism that helps to establish the "ground", the familiar aspects of context.

The Spatiotemporal Structure of Context

In some respects the far frontal resection produces memory disturbances characteristic of both hippocampectomy and amygdalectomy, though not so severe. Whereas medial temporal lobe ablations impair context formation by way of habituation of novel and familiar events, far frontal lesions wreak havoc on yet another contextual dimension, that of organizing the spatial and temporal structure of the context (Pribram, 1961; Anderson et al., 1976; Pribram et al., 1977).

The effect is best demonstrated by an experiment in which the normal scallop produced by a fixed interval schedule of reinforcement fails to develop and another in which the parameters of the classical alternation task were altered. Instead of interposing equal intervals between trials (go right, go left every 5 seconds) in the usual way, couplets of R/L were formed by extending the intertrial interval to 15" before each R trial (R5" L15" R5" L15" R5" L15"....). When this was done the performance of the far frontally lesioned monkeys improved immediately and was indistinguishable from that of the controls (Pribram & Tubbs, 1967; Pribram et al., 1977).

Figure 18 about here

This result suggests that for the subject with a bilateral far frontal ablation, the alternation task is experienced similarly to reading this page without any spaces between the words. The spaces, like the holes in doughnuts, provide the contextual structure, the parcellation or parsing of events by which the outside world can be coded and deciphered.

<u>Context as a Function of Reinforcing Contingencies</u>

Classically, disturbance of "working" short term memory has been ascribed to lesions of the frontal pole. Anterior and medial resections of the far frontal cortex were the first to be shown to produce impairment on delayed response and delayed alternation problems. In other tests of context-formation and fitting, frontal lesions also take their toll. Here also impairment of conditioned avoidance behavior and of classical conditioning, and of the orienting GSR is found. Furthermore, as shown in Figure 9, error sensitivity is reduced in an operant conditioning situation. After several years of training on mixed and multiple schedules, the animals were extinguished over four hours. The frontally lesioned animals failed to extinguish in the four-hour period, whereas the control monkeys did (Pribram, 1961). This failure in extinction accounts in part for poor performance in the alternation already described: The frontally lesioned animals again make many more repetitive errors. Even though they do not find a peanut, they go right back and keep looking (Pribram, 1959).

This result was confirmed and amplified in studies by Wilson (1962) and by Pribram et al. (1977) in which we asked whether errors followed alternation or non-reinforcement. A situation was devised in which both lids over two food wells opened simultaneously, but the monkey could obtain the peanut only if he had opened the baited well. Thus the monkey was given "complete" information on every trial and the usual correction technique could be circumvented. There were four procedural variations: correction-contingent, correction-noncontingent, noncorrection-contingent, and noncorrection-noncontingent. The contingency referred to whether the position of the peanut was altered on the basis of the monkey's responses (correct or incorrect) or whether its position was changed independently of the monkey's behavior. The relationship between each error was then analyzed. Table II shows that for the normal monkey the condition of reinforcement and nonreinforcement of the previous trial makes a difference. For the frontally lesioned monkey this is not the case. Change in location, however, affects both normal and frontal subjects about equally. In this situation, as well as in an automated computer controlled version of the alternatives problem, frontal subjects are simply uninfluenced by rewarding or nonrewarding consequences of their behavior.

Figure 19 about here.

In a multiple choice task (Pribram, 1959) (see Fig. 9) the procedure calls for a strategy of returning to the same object for five consecutive times, that is, to criterion, and then a shift to a novel item. The frontally lesioned animals are markedly deficient in doing this. Again, the conditions of reinforcement are relatively ineffective in shaping behavior in animals with frontal lesions and the monkeys' behavior becomes nearly random when compared to that of normal subjects (Pribram, Ahumada, Hartog & Roos, 1964). Behavior of the frontally lesioned monkeys thus appears to be minimally controlled by the expected outcome.

Transfer Learning

When we take a monkey who has learned to choose between circles of different sizes and ask him to transfer his experience to a situation in which he must choose among ellipses of different sizes (Bagshaw & Pribram, 1965) he will quickly master the new task unless he has a lesion of the limbic forebrain. This is not due to faulty generalization (Hearst & Pribram 1964a,b) --- generalization is impaired by lesions of the posterior cortical convexity. Rather, the difficulty stems from an inability to transfer what has been learned in one situation to another which is more or less similar. If his hippocampus has been resected bilaterally, the familiar cue will be normally effective only if it had previously been the rewarded one. The previously unrewarded cue will be reacted to as if it also were novel --- as if it had been completely ignored in the original discrimination problem. Just the opposite occurs when a monkey has been amygdalectomized. Now effective familiarity relates to non-reward (S ; negative instances); the previously rewarded cue is treated as novel in the transfer situation (Douglas & Pribram, 1966).

A variety of other problem situations have demonstrated this relationship between hippocampus and the previously non-reinforced (non-salient) aspects of a situation and between amygdala and prior reinforcement. Multiple choice (Douglas, Barrett, Pribram & Cerny, 1969) and distraction (Douglas & Pribram, 1966) experiments have been especially illuminating. In all instances, as in the reversal situations, whenever the probability structure of reinforcement becomes insufficiently distinct, or the distractions sufficiently powerful, limbic lesioned subjects fail to persist in a strategy that had proved useful in prior situations. Attention and search are no longer directed (programmed) by previous experience; hypothesis are no longer pursued (Pribram, Douglas & Pribram, 1969). The monkeys no longer expend the effort to maintain useful strategies

Summary:

Most approaches to the organization of learning and memory have relied on the elucidation of differences in terms of dichotomies, such as episodic *vs* semantic; procedural *vs* declarative; working *vs* referential. The temptation is to identify these dichotomies despite the fact that they stem from disparate data bases. The research resgults reported here suggest another approach, viz., a hierarchical arrangement of processes in a tree-like structure akin to computer programming. Figure 20 presents such an arrangement. The specifics must necessarily remain tentative but certain features of such a scheme are worth noting: At the base of each branch is a neural system whose operation has been identified in some considerable detail. What remains unclear is the anatomical and physiological natyure of the process which brings together the branches of the tree in the behaviorally determined higher-order nodes. Nor is it at present known how the various basic system programs address the distributed memory store, although suggestions (see Conclusion) have been tendered.

Figure 20 about here

Conclusion

When these decisional processes operate on the distributed memory store they re-member an input that had on earlier occasions become dismembered. The sensory-specific operators deal with recognition and with the processing of referentially meaningful information. The frontal lobe executive operators deal with recall and with the pragmatics of processing context sensitive, episode related instances (for review see, e.g., Pribram, 1971, 1977).

Both neuroscientists and cognitive psychologists currently frame their models in information processing terms. The data showing that decisional operators influence receptive field properties (Spinelli & Pribram, 1966; Pribram et al., 1981), though incomplete on this point are consonant with a proposal made by Gabor (1946), and extended by Brillouin (1962) and MacKay (1969), that the Fourier domain may become segmented into informational units called Logons by the operation of a "window" which limits band width. The interesting aspect of Gabor's proposal is that the window can be so adjusted that on some occasions processing occurs primarily in the holographic domain (leading to non-local operations such as translational invariance, object and size constancy, etc.) while on other occasions processing occurs in the space/time domain (leading to locating objects in time and space). Models such as Spinelli's (1970) content addressable and Pribram's Zoomar proposals (1971) are consonant with a Logon information processing approach, but more precise data are needed to establish the viability of this form of the information processing approach.

The persistent puzzle that brain functions appear to be both localized and distributed is thus resolved. Memory storage is shown to be distributed; decisional operators involved in coding and retrieval are localized. These operators can be conceived as separate brain systems, genetically inherent in their function but dependent on sensory input from the environment to trigger and shape their development (see, e.g., Chomsky, 1980; Pribram, 1971). In short, there are "boxes in the brain" --- each "box" corresponding to a "faculty of mind." But these "boxes" operate on a distributed matrix which is non-local and therefore available to all.

Perhaps the easiest way to conceptualize these problems is in terms of states and operators on those states. At present it appears reasonable to continue to search for linearities in the state descriptions of sensory perception, highly practiced skilled action and memory storage processes. These momentary states come under the control of localized non-linear operators whenever discriminative (e.g., recognition) or selective (planned) actions are involved. Whether these non-linearities are abstracted serially and hierarchically from the states, or whether they are imposed corticofugally by a parallel process --- or both --- continues to be an active area of investigation.

There is a considerable intellectual distance between Lashley's despair in finding a localized engram in 1950 and the richness of data and theory on cerebral localization and distribution in 1980 (Pribram, 1982). To his credit, Lashley recognized the problem and specified it in sufficient detail so the generation of investigators standing on his shoulders could deal effectively with it. That so much progress has been made reflects the support given by society to the brain and behavioral sciences during this 30-year period. Should this support continue, the issue of localization-distribution which has mobilized such differing views over the past two centuries may yet be resolved to everyone's satisfaction before the ending of the twentieth.

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FIGURE CAPTIONS

FIG. 1. Average number of errors made by a group of four monkeys whose primary visual cortex had been implanted with an epileptogenic agent (aluminum hydroxide cream). The first arrow indicates when implantations were made; the second when electrical seizure patterns commenced. Such electrical seizures (spike and dome) were recorded sporadically while the monkeys' visual discrimination performance remained above the 90% level.

FIG. 2. Visual discrimination learning curves of monkeys in whom electrical seizure patterns were induced by aluminum hydroxide implantations prior to the beginning of behavioral testing. Note the elongation of the period of stationarity and the similarity between slopes of the curves once learning has become manifest. This similarity is even more striking when backwards learning curves for individual subjects are compared.

FIG. 3. An elongated receptive field of a single cell in the visual cortex of a cat. This field was demonstrated despite the fact that the visual system was stimulated with visual white noise, i.e., with a spatiotemporally pseudorandom appearance of spots on an oscilloscope face. When the appearance of a spot in a certain location was correlated for approximately 30 msec with an increase (bright dot), decrease (no dot) or no change (avg dot) in the forming of the neuron, the receptive field pattern emerged.

FIG. 4. An inhibitory flank appears when the correlations performed as for those in Fig. 3 are carried out for approximately 40 msec. The 10-msec delay agrees with the results of intracellular recordings by Creutzfeld et al. (1974), who showed that the effect is due to lateral inhibition.

FIG. 5. A "Mexican hat" three-dimensional configuration of a receptive field of a single neuron in the lateral geniculate nucleus of a cat. The procedure by which such receptive fields are plotted is detailed in the legend of Figure 6.

FIG. 6. The method by which a receptive field is plotted is shown. A computer controls the location of a spot and correlates the number of impulses (recorded by a) emitted by the neuron while the spot is in that location. The Mexican hat configuration shown in Fig. 5 results when the plane on which the spot is displayed is represented by the x and y axes and the number of impulses by the z axis. When the crown of the hat is sectioned parallel to the brim, two standard deviations above background activity, the ordinarily shown two-dimensional circular-surround (excitatory-inhibitory) receptive field results. This concentric receptive field arrangement is seen at the right of the figure.

FIG. 7. When the procedure detailed in Fig. 6 is performed with recordings from a cortical cell in the visual system, the elongated receptive field with inhibitory flank(s) similar to that in Figs. 3 and 4 is obtained. The elongation of the receptive field accounts for the fact that lines are the preferred stimulus to activate the cortical cells.

FIG. 8. When lines are used to define the cortical receptive field, the lines may vary in width and spacing. Such variations are designated as changes in spatial frequency in cycles/degree. Tuning curves for cortical cells are obtained by stimulating the visual system with gratings (multiple lines) of varying spatial frequency. The tuning curves obtained in the study presented in this figure were obtained with above-threshold stimulation (and remained unchanged by electrical stimulation of frontal and posterior brain systems).

FIG. 9. Tuning curves obtained in the manner described in the legend for Fig. 8, but at contrast threshold. From DeValois & DeValois, 1980.

Fig. 10. Comparison of tuning curves (for cat, left and monkey, right) obtained as above with those obtained when a single line of varying width is used to stimulate the visual system. Note that the line can be considerably broadened without any change in its output. This indicates that the cell is better tuned to spatial frequency than to lines per se. See text for additional experiments which support this finding.

FIG. 11. Average number of repetitive errors made by three groups of monkeys (normal controls, monkeys with inferotemporal and with far frontal resections) while searching for a peanut hidden under one one of several (2 to 12) junk objects. Note the changes in the curves of the controls and inferotemporal resected monkeys and that for the lower number of cues that the controls are performing better than the monkeys with inferotemporal resections. For an explanation of this result, see Fig. 12. Note also that the monkeys with far frontal resections were immediately attracted to the novel cue which covered the peanut in each situation, thus making few repetitive search errors. See also Fig. 19.

FIG. 12. The explanation for the results obtained in Fig. 11 is that the monkeys with resections of the inferotemporal cortex restricted their sampling to a limited range of cues, thus gaining a temporary advantage over the normal control subjects.

FIG. 13. Graphs of the actual learning curves of three monkeys mastering a discrimination which involved three separable features. Note how performance is enhanced as each non-rewarded feature is discriminated and eliminated from the response repertoire.

FIG. 14. Reconstructions of the brains of monkeys whose inferotemporal cortex has been cross-hatched. For the results on behavioral testing see Fig. 16.

FIG. 15. Reconstructions of the brains of monkeys whose inferotemporal cortex has been undercut. The composit figure shows both the area common to all cuts (black) and the sum of all the undercut areas. For the effects on behavioral testing see Fig. 16.

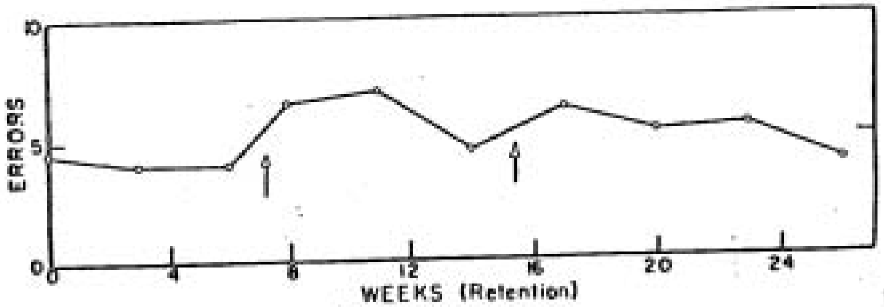
FIG. 16. The behavioral results of cross-hatching and undercutting the inferotemporal cortex. Note the absence of the effects of cross-hatching and the severe deficits resulting from undercutting.

FIG. 17. Representation of the mediobasal motorcortex: The cortical points on the mediobasal surface of the monkey brain from which changes in blood pressure, heart and respiratory rate are obtained on electrical stimulations. Top: lateral view. Bottom: mediobasal view.

FIG. 18. The learning curves of monkeys with reactions of the far frontal cortex and their unoperated normal controls on a delayed alternation task in which the delay period was made asymmetrical (5 sec; 15 sec). Note the excellent performances of the subjects with the resection and that they failed the symmetrical delay (5 sec; 5 sec) task despite having been given much experience (1000 trails) on this task.

FIG. 19. Graph showing the number of trials taken to come to criterion after finding the peanut in the multiple task by monkeys with far frontal and inferotemporal cortex resections and a normal control group. Note that only the far frontal group repeatedly examined objects which covered no peanut despite their having found the object which did cover a peanut. See also Figs. 11 and 12.

FIG. 20. Diagram of the relationships among types of learning and memory processes. Note that the functions of the neural systems described in this chapter make up the endpoints of each of the branches of the tree. The term contextual is used in preference to such terms as working memory (based on the alternation paradigm); declarative (based on computer programming paradigms); or pragmatic (based on linguistic paradigms) because it is more general in meaning. The term referential is used, where in linguistics and cognitive psychology the term semantic would apply.



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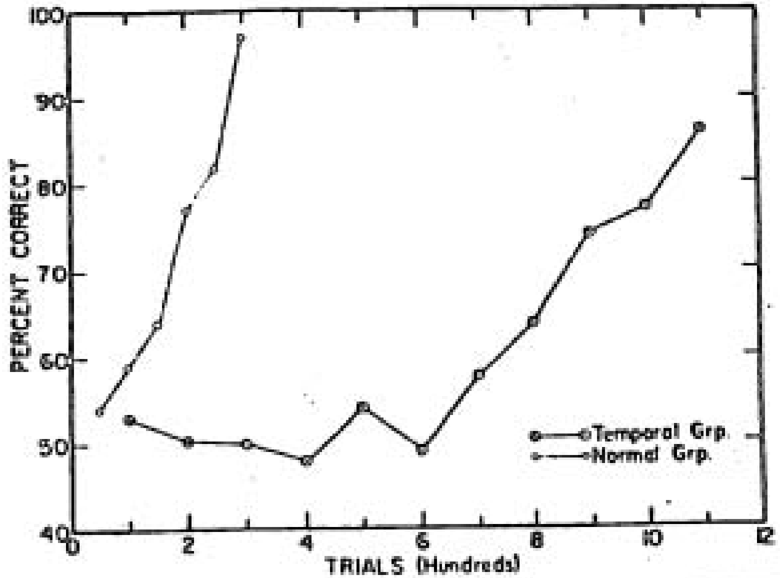
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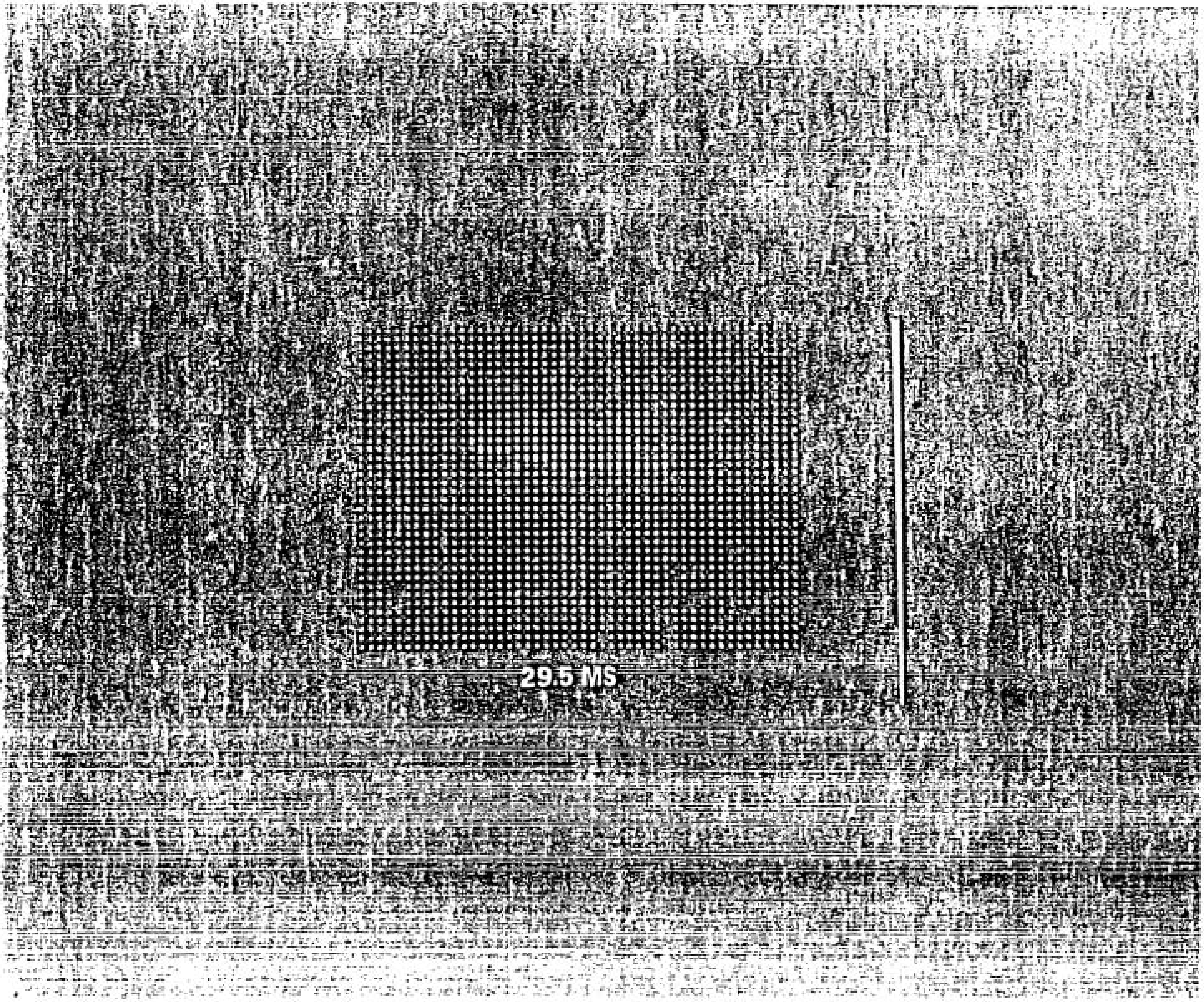
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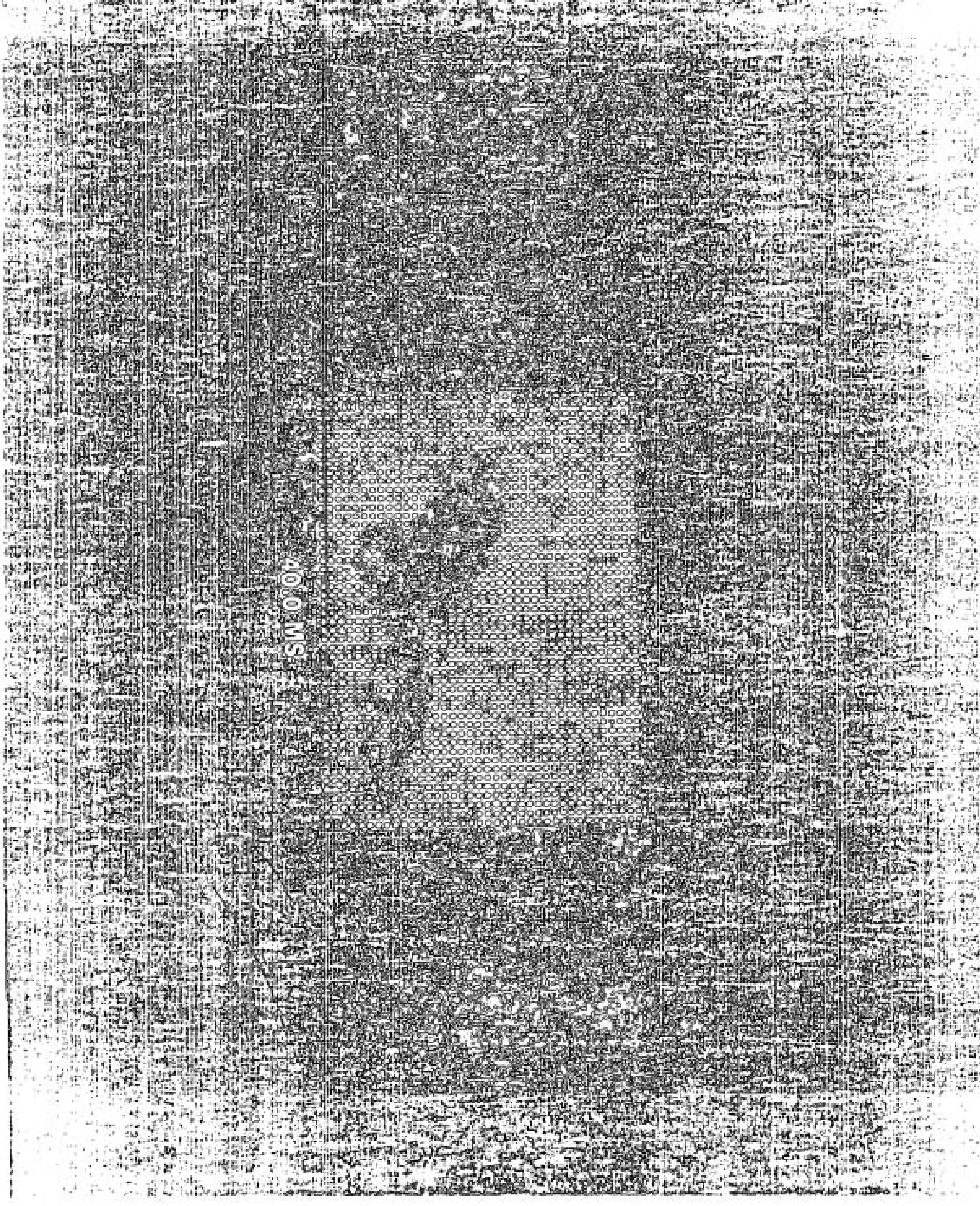
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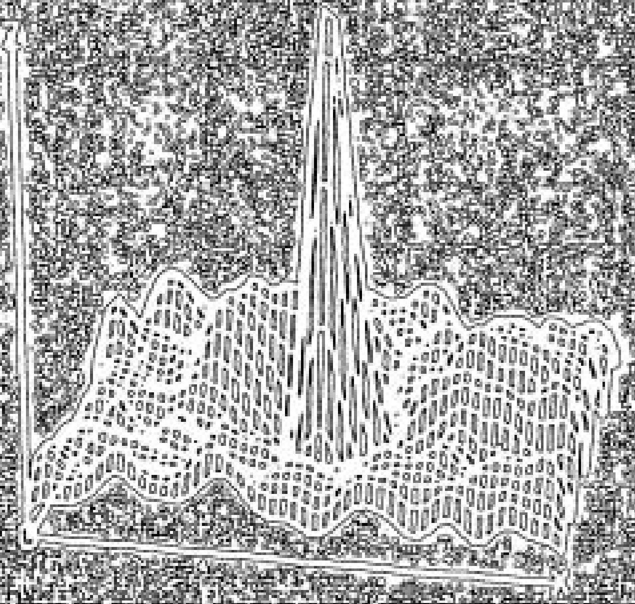
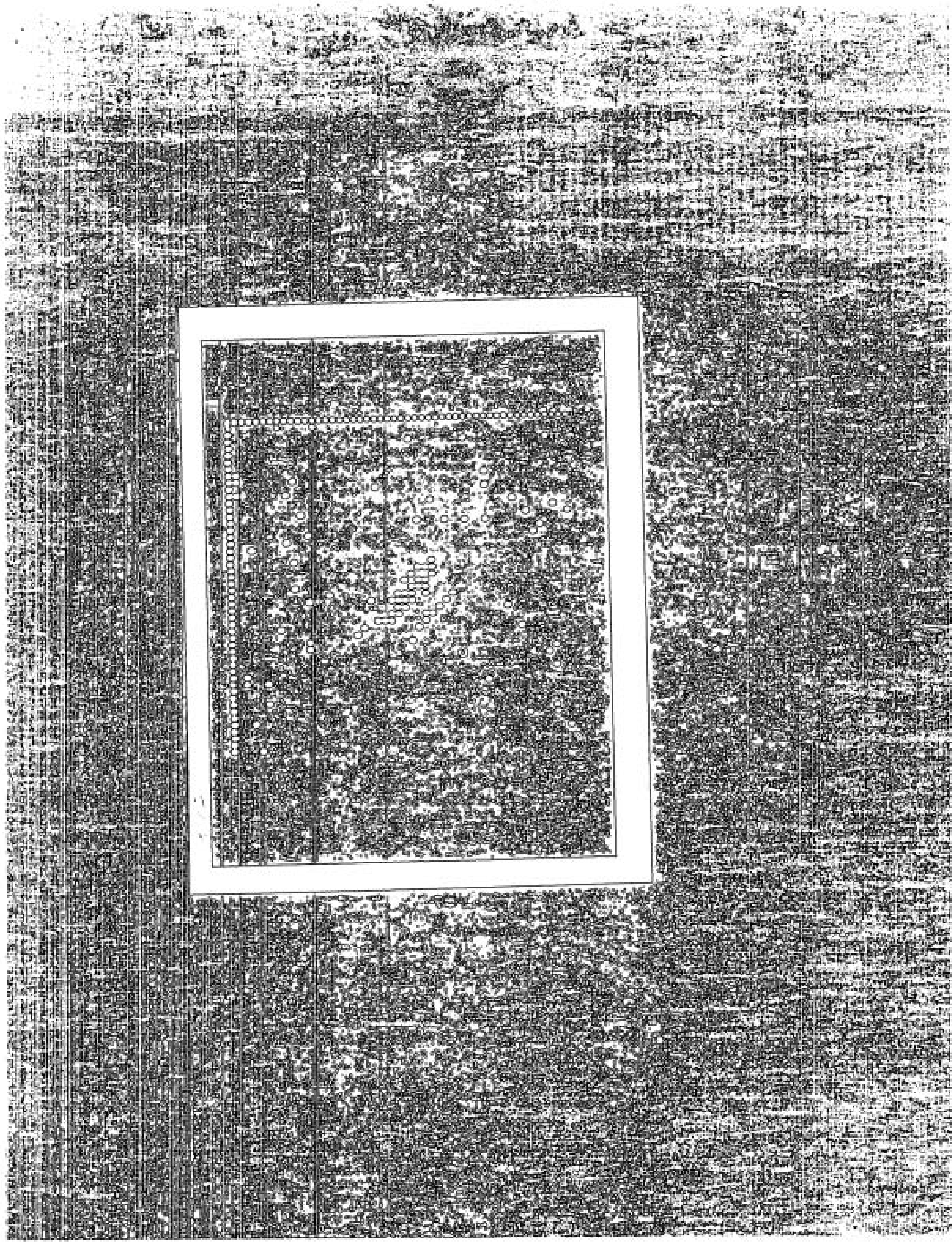
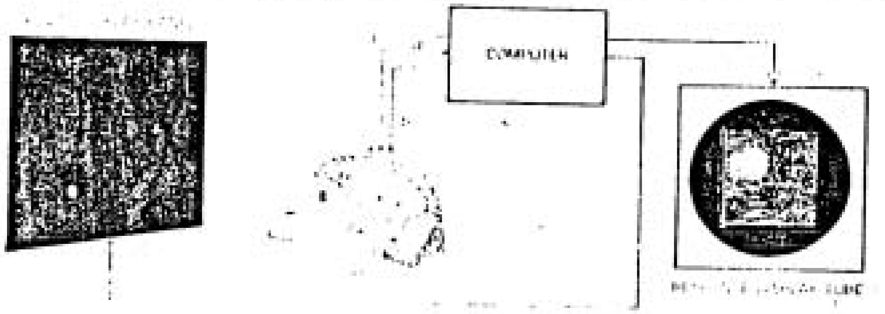


Fig 5

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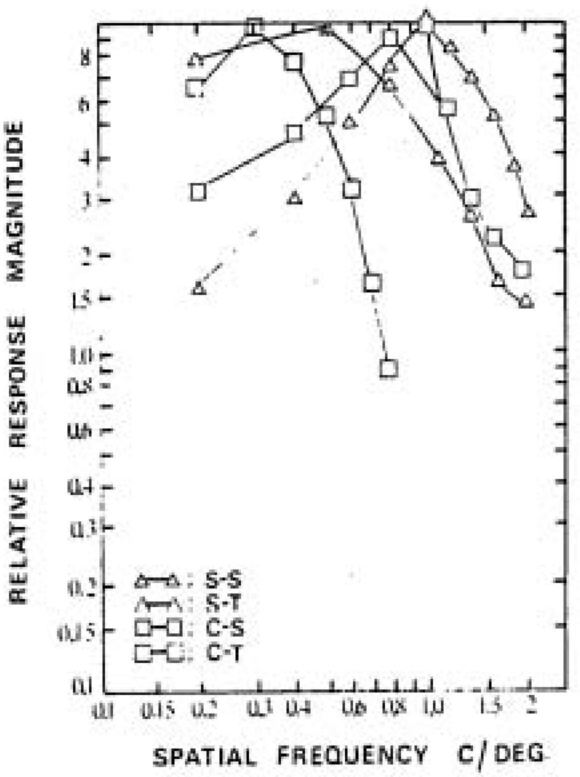
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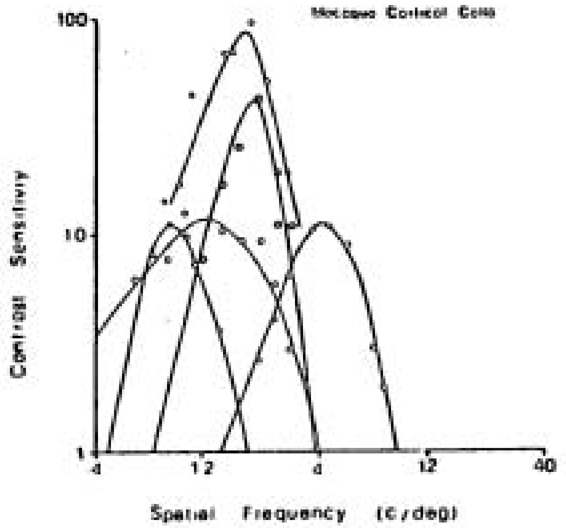
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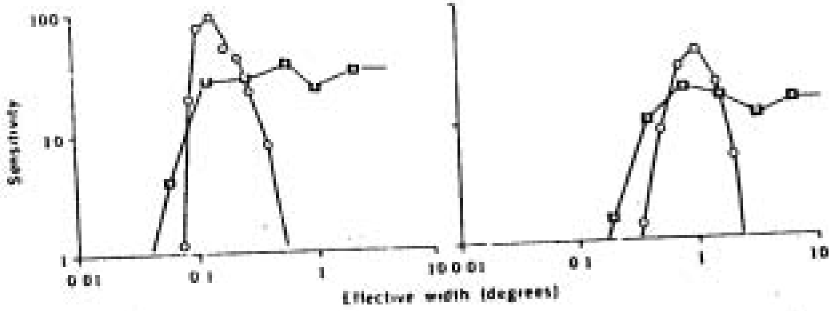
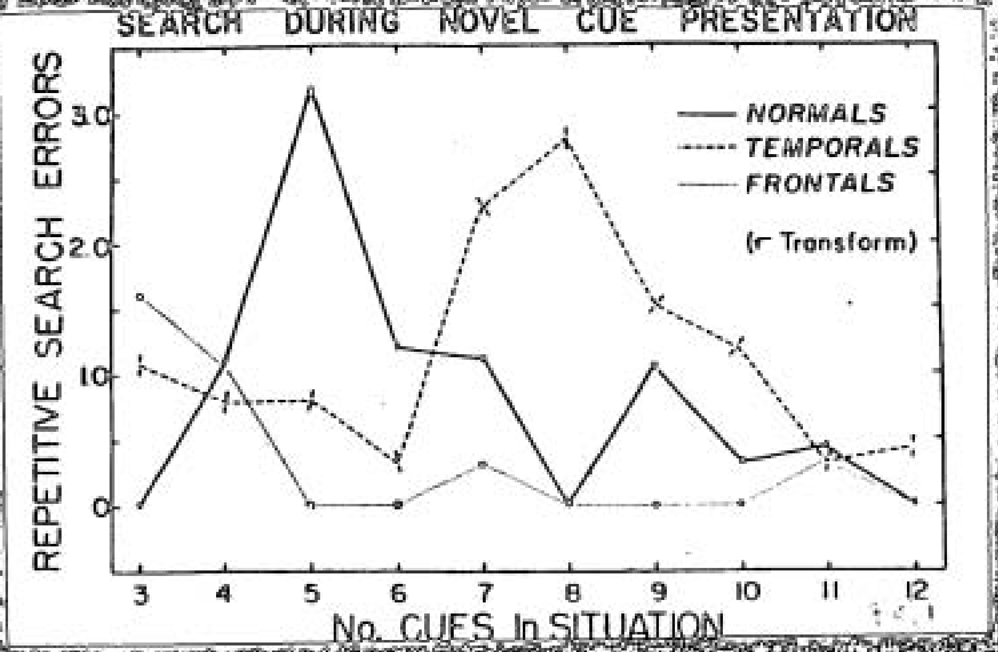
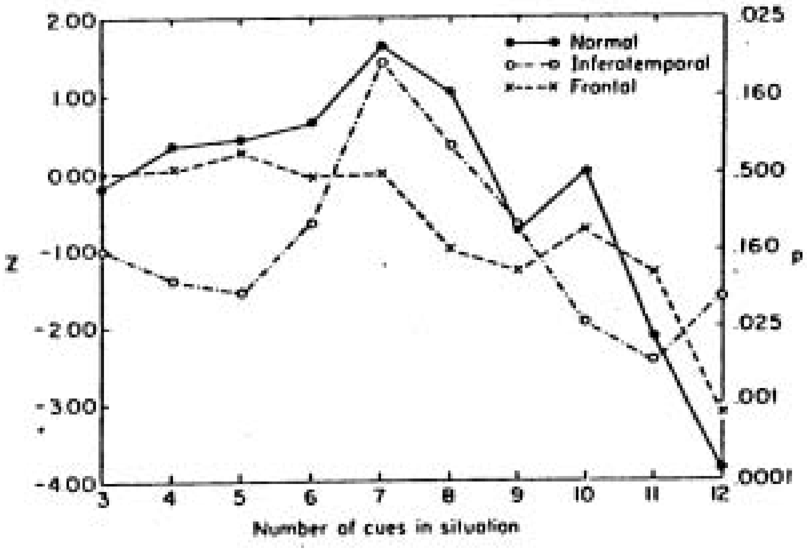
40
Spatial Frequency (c/deg)

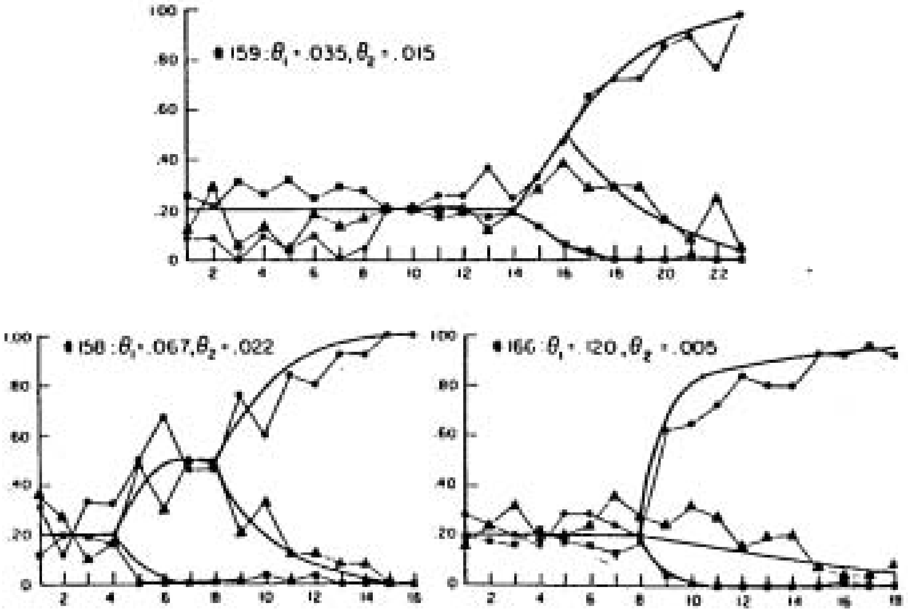


100
10
1
Sensitivity
0.01
0.1
1
10 0.01
0.1
1
10
Effective width (degrees)

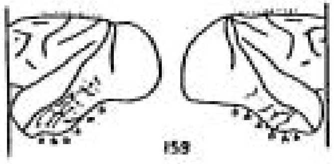
Fig. 10


SEARCH DURING NOVEL CUE PRESENTATION
NORMALS
TEMPORALS
FRONTALS
(r Transform)
REPETITIVE SEARCH ERRORS
3.0
2.0
1.0
0
3
4
5
6
7
8
9
10
11
12
No. CUES In SITUATION

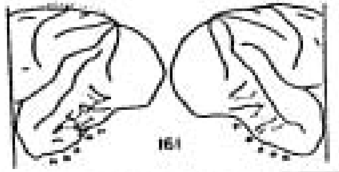

Normal
Inferotemporal
Frontal
Z
2.00
1.00
0.00
-1.00
-2.00
-3.00
-4.00
.025
.160
.500
.160
.025
.001
.0001
p
3
4
5
6
7
8
9
10
11
12
Number of cues in situation



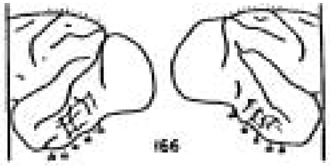
#159: θ_1 = .035, θ_2 = .015
1.00
.80
.60
.40
.20
0
2
4
6
8
10
12
14
16
18
20
22
#158: θ_1 = .067, θ_2 = .022
1.00
.80
.60
.40
.20
0
2
4
6
8
10
12
14
16
#166: θ_1 = .120, θ_2 = .005
1.00
.80
.60
.40
.20
0
2
4
6
8
10
12
14
16
18



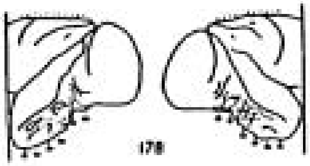
159



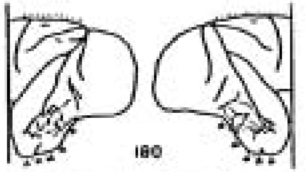
161



166

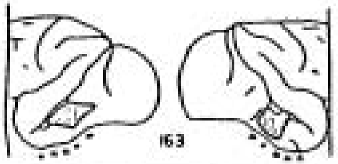


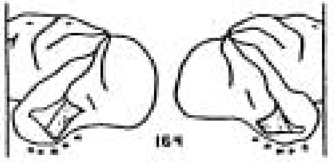
178

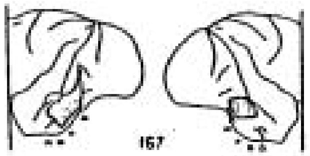


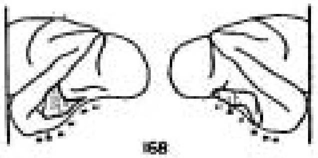
180

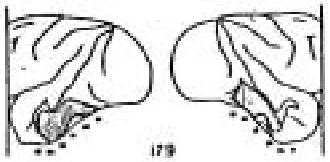
Fig 14


163


164


167


168


179


COMPOSITE

	Animal	3 vs. 0	0 vs. 6	3 vs. 0
Crosshatch	158	380	80	0
	159	180	100	0
	161	580	50	0
	166	130	0	0
Undercut	163	[1014]	100	300
	164	[1030]	200	[500]
	167	704	50	0
	168	[1030]	150	[500]
Normal	160	280	100	0
	162	180	100	0
	165	280	100	0
	170	350	100	0

Fig 16

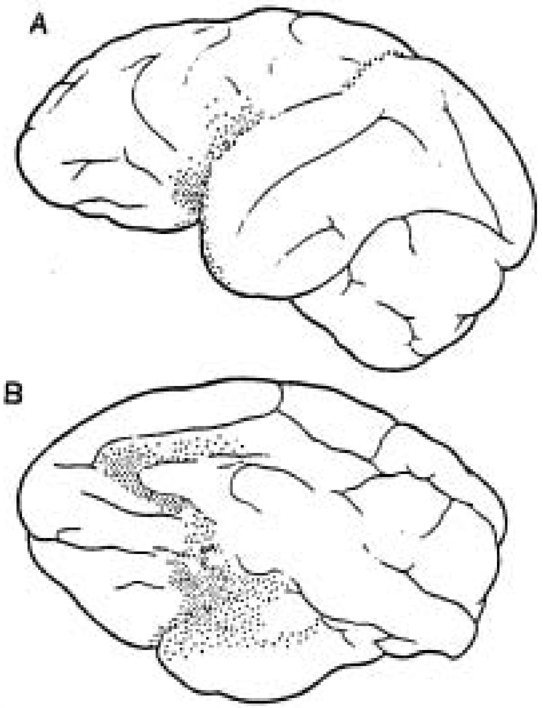
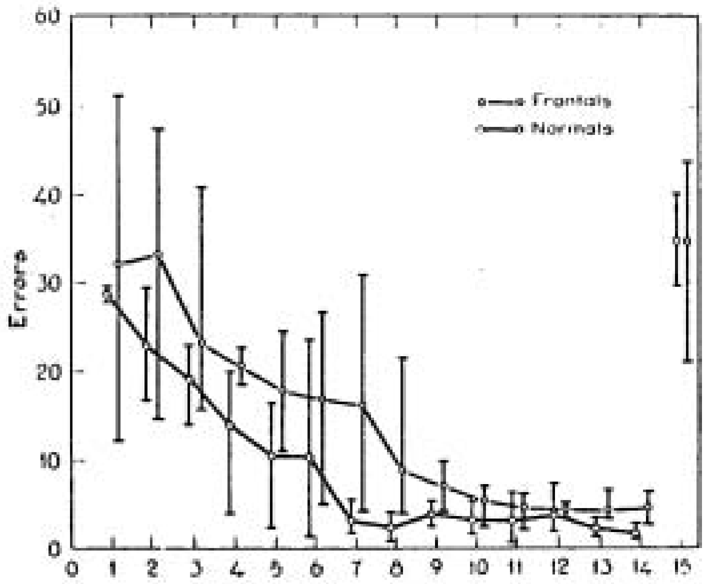


Fig. [illegible]


Errore
0
10
20
30
40
50
60
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Frontals
Normals

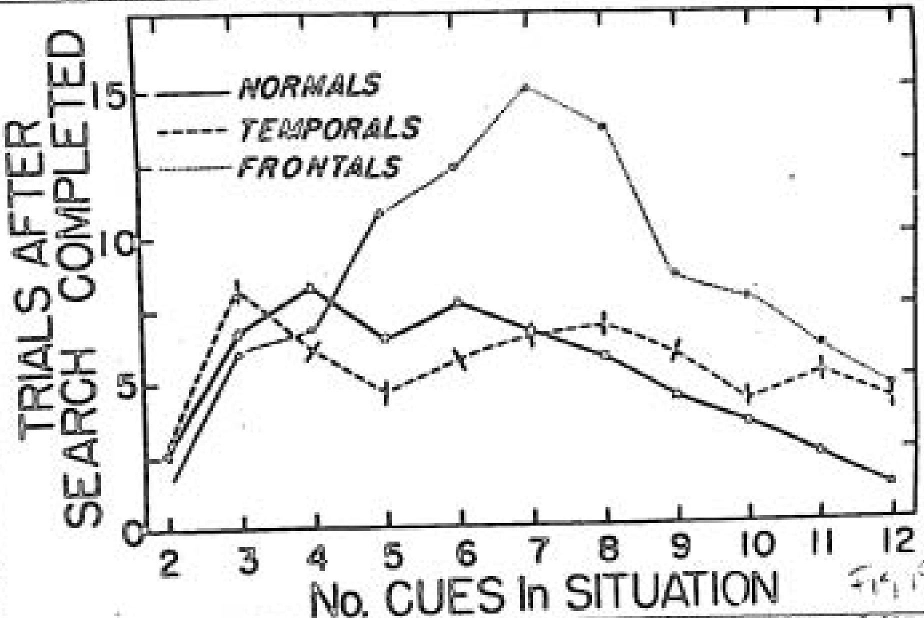
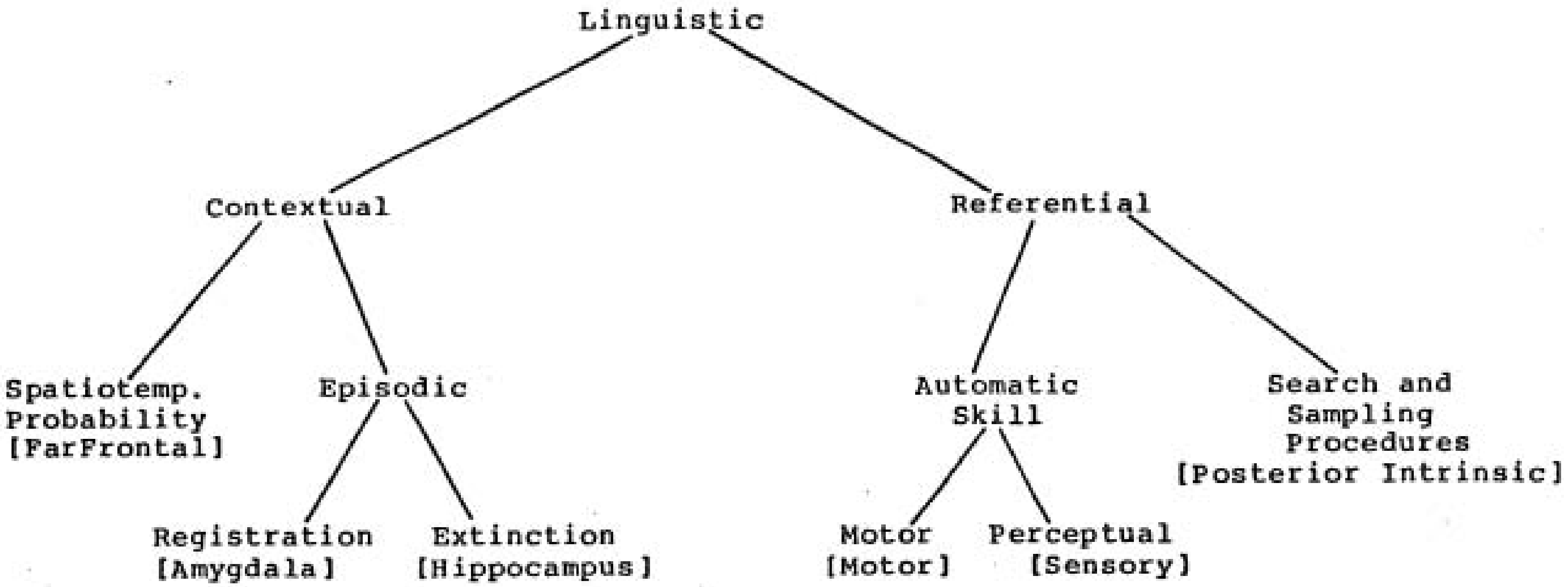

TRIALS AFTER SEARCH COMPLETED
0
5
10
15
NORMALS
TEMPORALS
FRONTALS
2
3
4
5
6
7
8
9
10
11
12
No. CUES In SITUATION

Fig 5


Linguistic
Contextual
Referential
Spatiotemp. Probability [FarFrontal]
Episodic
Automatic Skill
Search and Sampling Procedures [Posterior Intrinsic]
Registration [Amygdala]
Extinction [Hippocampus]
Motor [Motor]
Perceptual [Sensory]