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Image, Information, and Episodic Modes of Central Processing

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Introduction

Over the past 25 years, research on the brain mechanisms involved in learning and remembering has been rewarding beyond expectation. It was only a little over 25 years ago that Lashley uttered his famous remark that, on the basis of his lifetime of research on brain function, it was clear that "learning just could not take place." Nor was Pavlov any more successful in delineating by direct intervention in brain mechanisms the processes he and his students had so painstakingly elaborated with behavioral techniques.

All this is now changed as can be seen from the contents of this volume. In my contribution, I wish to review evidence that has accumulated around two problems. One concerns brain mechanisms in image processing and the resulting distributed semantic store. The other deals with a distinction between information and episodic processing as two different modes of learning and remembering.

Image Processing and the Distributed Memory Store

Lashley's despair was produced by his repeated findings of equivalence of function of parts of brain systems. Not only was he unable to excise any specific memory, but he was also unable to account for the facts of sensory and motor equivalence:

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These three lines of evidence indicate that certain coordinated activities, known to be dependent upon definite cortical areas, can be carried out by any part (within undefined limits) of the whole area. Such a condition might arise from the presence of many duplicate reflex pathways through the areas and such an explanation will perhaps account for all of the reported cases of survival of functions after partial destruction of their special areas, but it is inadequate for the facts of sensory and motor equivalence. These facts establish the principle that once an associated reaction has been established (e.g., a positive reaction to a visual pattern), the same reaction will be elicited by the excitation of sensory cells which were never stimulated in that way during the course of training. Similarly, motor acts (e.g., opening a latch box), once acquired, may be executed immediately with motor organs which were not associated with the act during training [Lashley, 1960, p. 240. Used with permission of McGraw-Hill Book Company].

What sort of brain mechanism could be imagined that would account for the principle that "once an associated reaction has been established, the same reaction will be elicited by the excitation of sensory cells which were never stimulated in that way during the course of training"? And what mechanism could be devised to deal with the fact that "motor acts, once acquired, may be executed immediately with motor organs which were not associated with the act during training"? What sort of mechanism of association could be taking place during learning so that its residual would, as it were, act at a distance?

The difficulties of conceptualization may be summarized as follows: During acquisition, associative processes must be operative. However, these associative processes must result in a distributed store. On the basis of Lashley's analysis, input must become dismembered before it becomes remembered. Association and distribution are in some fundamental way inexorably linked.

During the mid-1960s it became apparent that image processing through holography could provide a model for a mechanism with such "distribution by association" properties. As in the case of every novel approach, there were, of course, earlier formulations including those of Lashley that attempted to explain these aspects of brain function in terms that today we would call holographic.

Historically the ideas can be traced to problems posed during neurogenesis when the activity of relatively remote circuits of the developing nervous system must become integrated to account for such simple behaviors as swimming. Among others, the principle of chemical "resonances" that "tune" these circuits has had a long and influential life (see, e.g., Loeb, 1907; Weiss, 1939). More specifically, however, Goldscheider (1906) and Horton (1925) proposed that the establishment of tuned resonances in the form of interference patterns in the adult brain could account for a variety of perceptual phenomena. More recently, Lashley (1942) spelled out a mechanism of neural interference patterns to explain stimulus

equivalence and Beurle (1956) developed a mathematically rigorous formulation of the origin of such patterns of plane wave interferences in neural tissue. But it was not until the advent of holography with its powerful damage-resistant image storage and reconstructive capabilities that the promise of an interference pattern mechanism of brain function became fully appreciated. As the properties of physical holograms became known (see Collier, Burckhardt, & Lin, 1971; Goodman, 1968; Stroke, 1966), a number of scientists saw the relevance of holography to the problems of brain function, memory, and perception (e.g., Baron, 1970; Cavanagh, 1972; Julesz & Pennington, 1965; Kabrisky, 1966; Pribram, 1966; van Heerden, 1963; Westlake, 1968).

The advent of these explanations came with the development of physical holography (e.g., Stroke, 1966) from the mathematical principles enunciated by Gabor (1948). Equally important, however, was the failure of computer science to simulate perception and learning in any adequate fashion. The problem lies in the fact that computer-based "perceptions" (e.g., Rosenblatt, 1962) were constructed on the basis of an assumed random connectivity in neural networks when the actual anatomical situation is essentially otherwise. In the visual system, for instance, the retina and cortex are connected by a system of fibers that run to a great extent in parallel. Only two modifications of this parallelity occur.

1. The optic tracts and radiations that carry signals between the retina and cortex constitute a sheaf within which the retinal events converge to some extent onto the lateral geniculate nucleus of the thalamus from where they diverge to the cortex. The final effect of this parallel network is that each fiber in the system connects ten retinal outputs to about 5000 cortical receiving cells.
2. In the process of termination of the fibers at various locations in the pathway, an effective overlap develops (to about 5 degrees of visual angle) between neighboring branches of the conducing fibers.

Equally striking and perhaps more important than these exceptions, however, is the interpolation at every cell station of a sheet of horizontally connected neurons in a plane perpendicular to the parallel fiber system. These horizontal cells are characterized by short or absent axons but spreading dendrites. It has been shown in the retina (Werblin & Dowling, 1969) and to some extent also in the cortex (Creutzfeldt, 1961) that such spreading dendritic networks may not generate nerve impulses; in fact, they usually may not even depolarize. Their activity is characterized by hyperpolarization that tends to organize the functions of the system by inhibitory rather than excitatory processes. In the retina, for instance, no nerve impulses are generated prior to the (amacrine and) ganglion cells from which the optic nerve fibers originate. Thus, practically all of the complexity manifest in the optic nerve is a reflection of the organizing

properties of depolarizing and hyperpolarizing events, not of interactions among nerve impulses.

Two mechanisms are therefore available to account for the distribution of signals within the neural system. One relies on the convergence and divergence of nerve impulses onto and from a neuronal pool. The other relies on the presence of lateral (mostly inhibitory) interactions taking place in sheets of horizontal dendritic networks situated at every cell station perpendicular to the essentially parallel system of input fibers. Let us explore the possible role of both these mechanisms in explaining the results of the lesion studies.

Evidence is supplied by experiments in which conditions of anesthesia are used that suppress the functions of small nerve fibers, thus leaving intact and clearly discernible the connectivity by way of major nerve impulse pathways. These experiments have shown that localized retinal stimulation evokes a receptive field at the cortex over an area no greater than a few degrees in diameter (e.g., Talbot & Marshall, 1941). Yet, the data that must be explained indicate that some 80% or more of the visual cortex including the foveal region can be extirpated without marked impairment of the recognition of a previously learned visual pattern. Thus, whatever the mechanisms, distribution of input cannot be due to the major pathways, but must involve the fine-fibered connectivity in the visual system, either via the divergence of nerve impulses and/or via the interactions taking place in the horizontal cell dendritic networks.

Both are probably responsible to some extent. Remember that nerve impulses occurring in the fine fibers tend to decrement in amplitude and speed of conduction, thus becoming slow, graded potentials. Furthermore, these graded slow potentials or minispikes usually occur in the same anatomical location as the horizontal dendritic inhibitory hyperpolarizations and thus interact with them. In fact, the resulting microorganization of junctional neural activity (synaptic and ephaptic) could be regarded as a simple summation of graded excitatory (depolarizing) and inhibitory (hyperpolarizing) slow potential processes.

These structural arrangements of slow potentials are especially evident in sheets of neural tissue such as in the retina and the cortex. The cerebral cortex, for instance, may be thought of as consisting of columnar units that can be considered more or less independent basic computational elements, each of which is capable of performing a similar computation (Hubel & Wiesel, 1968; Mountcastle, 1957). Inputs to the basic computational elements are processed in a direction essentially perpendicular to the sheet of the cortex, and therefore cortical processing occurs in stages, each stage transforming the activation pattern of the cells in one of the cortical layers to the cells of another cortical layer. Analyses by Kabrisky (1966) and by Werner (1970) show that processing by one basic computational element remains essentially within that element, and therefore the cortex can be

considered to consist of a large number of essentially similar parallel processing elements. Furthermore, the processing done by any one of the basic computational elements is itself a parallel process (see, for example, Spinelli, 1970), with each layer transforming the pattern of activity that arrived from the previous layer by the process of temporal and spatial summation, that is, the summation of slow hyperpolarization and depolarization in the dendritic microstructure of the cortex. Analyses by Ratliff (1965) and Rodieck (1965) have shown that processing (at least at the sensory level) that occurs through successive stages in such a layered neural network can be described by linear equations. Each computational element is thus capable of transforming its inputs through a succession of stages, and each stage produces a linear transformation of the pattern of activity at the previous stage.

Let us trace in detail the evidence regarding these stages in the visual system. Quantitative descriptions of the interactions that occur in the retina are inferred from the output of ganglion cells from which receptive field configurations are recorded by making extracellular microelectrode recordings from the optic nerve. The retinal interactions per se take place initially by virtue of local graded slow-wave potentials—hyperpolarizations and depolarizations that linearly sum within the networks of receptors, bipolar, and horizontal cells from which nerve impulses are never recorded. The receptive fields generated by these graded potential changes display a more or less circular center surrounded by a ring of activity of a sign opposite that of the center. This configuration has been interpreted to mean that the activity of a receptive neuron generates inhibition in neighboring neurons through lateral connectivities (e.g., Békésy, 1967; Hartline, Wagner, & Ratliff, 1956; Kuffler, 1953) perpendicular to the input channels. In view of the fact that no nerve impulses can be recorded from the cells (e.g., horizontal) that mediate the lateral inhibition, the inference can be made that the interactions among graded potentials, waveforms, are responsible (Pribram, 1971; Pribram, Nuwer, & Baron, 1974). Such waveforms need not be thought of as existing in an unstructured homogenous medium. The dendritic arborizations in which the gradual potential changes occur can act as structural wave guides. However, as Beurle (1956) has shown, such a structural medium can still give rise to a geometry of plane waves provided the structure is reasonably symmetrical. The mathematical descriptions of receptive field configurations bear out Beurle's model. Such descriptions have been given by Ratliff (1965) and Rodieck (1965). Mathematically, they involve a convolution of luminance change of the retinal input with the inferred inhibitory characteristics of the network to compose the observed ganglion cell receptive field properties.

The gist of these experimental analyses is that the retinal mosaic becomes decomposed into an opponent process by depolarizing and hyperpolarizing slow potentials and transforms into more or less concentric re-

ceptive fields in which center and surround are of opposite sign. Sets of convolutional integrals fully describe this transformation.

The next cell station in the visual pathway is the lateral geniculate nucleus of the thalamus. The receptive field characteristics of the output from neurons of this nucleus are in some respects similar to the more or less concentric organization obtained at the ganglion cell level. Now, however, the concentric organization is more symmetrical, the surround has usually more clear-cut boundaries and is somewhat more extensive (e.g., Spinelli & Pribram, 1967). Furthermore, a second penumbra of the same sign as the center can be shown to be present, although its intensity (number of nerve impulses generated) is not nearly so great as that of the center. Occasionally, a third penumbra, again of opposite sign, can be made out beyond the second (Hammond, 1972).

Again, a transformation has occurred between the output of the retina and the output of the lateral geniculate nucleus. This transformation apparatus appears to act as a rectification process. Each geniculate cell thus acts as a peephole "viewing" a part of the retinal image mosaic. This is due to the fact that each geniculate cell has converging upon it some 10,000 ganglion cell fibers. This receptive field peephole of each geniculate cell is made of concentric rings of opposing sign, whose amplitudes fall off sharply with distance from the center of the field. In these ways the transformation accomplished is like very near-field optics that describes a Fresnel hologram.

Pollen, Lee, and Taylor (1971), although supportive of the suggestion that the visual mechanism as a whole may function in a holographiclike manner, emphasize that the geniculate output is essentially topographic and punctate, is not frequency specific, and does not show translational invariance; that is, every illuminated point within the receptive field does not produce the same effect. Furthermore, the opponent properties noted at the retinal level of organization are maintained and enhanced at the cost of overall translational invariance. Yet a step toward a discrete transform domain has been taken since the output of an individual element of the retinal mosaic—a rod or cone receptor—is the origin of the signal transformed at the lateral geniculate level.

When the output of lateral geniculate cells reaches the cerebral cortex, further transformations take place. One set of cortical cells, christened "simple" by their discoverers (Hubel & Wiesel, 1968), has been suggested to be characterized by a receptive field organization composed by a literally linelike arrangement of the outputs of lateral geniculate cells. This proposal is supported by the fact that the simple-cell receptive field is accompanied by side bands of opposite sign and occasionally by a second side band of the same sign as the central field. Hubel and Wiesel proposed that these simple cells thus serve as line detectors in the first stage of a hierarchical arrangement of pattern detectors. Pollen *et al.* (1971) have

countered this proposal on the basis that the output from simple cells varies with contrast luminance as well as orientation and that the receptive field is too narrow to show translational invariance. They therefore argue that an ensemble of simple cells would be needed to detect orientation. They suggest that such an ensemble would act much as the strip integrator used by astronomers (Bracewell, 1965) to cull data from a wide area with instruments of limited topographic capacity (as is found to be the case in lateral geniculate cells).

Another class of cortical cells has generated great interest. These cells were christened "complex" by their discoverers, Hubel and Wiesel, and thought by them (as well as by Pollen) to be the next step in the images processing hierarchy. Some doubt has been raised (Hoffman & Stone, 1971) because of their relatively short latency of response as to whether all complex cells receive their input from simple cells. Whether their input comes directly from the geniculate or by way of simple cell processing, however, the output from complex cells of the visual cortex displays transformations of the retinal input, characteristics of the holographic domain.

A series of elegant experiments by Fergus Campbell and his group (1974) have suggested that these complex cortical cells are spatial-frequency sensitive elements. Initially, Campbell showed that the response of the potential evoked in man and cat by repeated flashed exposure to a variety of gratings of certain spacing (spatial frequency) adapted not only to that fundamental frequency but also to any component harmonics present. He therefore concluded that the visual system must be encoding spatial frequency (perhaps in Fourier terms) rather than the intensity values of the grating. He showed further that when a square wave grating was used, adaptation was limited to the fundamental frequency and its third harmonic as would be predicted by Fourier theory. Finally, he found neural units in the cat's cortex that behaved as did the gross potential recordings.

Pollen (1973) has evidence that suggests that these spatial-frequency sensitive units are Hubel and Wiesel's complex cells, although both his work and that of Maffei and Fiorentini (1973) have found that simple cells also have the properties of spatial frequency filters, in that they are sensitive to a selective band of spatial frequencies. In addition, the latter investigators have found that the simple cells can transmit contrast and spatial phase information in terms of two different parameters of their response: Contrast is coded in terms of impulses per second and spatial phase in terms of firing pattern.

The receptive field of complex cells is characterized by the broad extent (when compared with simple cells) over which a line of relatively indeterminate length but a certain orientation will elicit a response. Pollen demonstrated that the output of complex cells was not invariant to orientation alone—number of lines and their spacing also appeared to influence response. He concluded, therefore, as had Fergus Campbell, that

these cells were spatial-frequency sensitive and that the spatial-frequency domain was fully achieved at this level of visual processing. Additional corroborating evidence has recently been presented from the Pavlov Institute of Physiology in Leningrad by Glezer, Ivanoff, and Tscherbach (1973), who relate their findings on complex receptive fields as Fourier analyzers to the dendritic microstructure of the visual cortex much as we have done here.

Even more recently, series of studies from the Cambridge laboratories, from MIT, Berkeley, and Stanford University, have substantiated the earlier reports. Pribram, Lassonde, and Ptito (in preparation) have confirmed that both simple and complex cells are selective to restrictive bandwidths of spatial frequencies, but that simple cells encode spatial phase, whereas complex cells do not. Thus simple cells may be involved in the perception of spatial location, whereas complex cells are more truly "holographic" in that they are responsible for translational invariance. Schiller, Finlay, and Volman (1976a,b,c,d) have performed a comprehensive coverage of receptive field properties, including spatial frequency selectivity. Movshon, Thompson, and Tolhurst (1978a,b,c) in another set of experiments showed that receptive fields could be thought of as spatial filters (much as van Heerden, 1963, originally proposed) whose Fourier transform mapped precisely the cell's response characteristics. De Valois, Albrecht, and Thorell (1978) have taken this work even a step further by showing that whereas these cells are tuned to from .5 to 1.5 octaves of bandwidth of the spatial frequency spectrum, they are not tuned at all to changes in bar width. Finally, De Valois has tested whether the cells are selective of edges making up patterns or their Fourier transforms. The main components of the transforms of checkerboards and plaids lie at different orientations from those of the edges making up the patterns. In every case the orientation of the checkerboards or plaids had to be rotated to match the Fourier encoding and the rotation was to exact amount in degrees and minutes of arc predicted by the Fourier transform.

The results of these experiments go a long way toward validating the holographic hypothesis of brain function. However, as I have noted previously (Pribram, Nuwer, & Baron, 1974) a major problem remains even after these data are incorporated in the construction of a precise model. Each receptive field, even though it encodes in the frequency domain, does so over a relatively restricted portion of the total visual field. Robson (1975) has thus suggested that only a "patch" of the field becomes "Fourier" represented. However, this major problem has now been resolved and the solution has brought unexpected dividends. Ross (see review by Leith, 1976) has constructed holograms on the principles proposed by Bracewell (1965) and espoused by Pollen (see Pollen & Taylor, 1974). Such multiplex or strip integral holograms are now commercially available (Multiplex Co., San Francisco, California). Not only do they display all the properties of

ordinary holograms, but also can be used to encode movement as well.
Thus, by combining frequency encoding with a spatial "patch" or "slit"
representation, a lifelike, three-dimensional moving image can be con-
structed.

Although detailed specification has been given for the visual system
only, the foregoing analysis is in large part also relevant to the auditory
system, the tactile system, and the motor system (see Pribram, 1971, for
review). The recently accumulated facts concerning the visual system are
the most striking because it was not suspected that spatial pattern per-
ception would be found to be based on a stage that involves frequency
analysis. The finding of the ubiquity of frequency analysis by brain tissue
has made accessible explanations of hitherto inexplicable observations, such
as the distributed nature of the memory trace and the projection of images
away from the surface in which their representation has become encoded.
The model has had considerable explanatory power.

Information and Episodic Processing

Whenever a powerful explanatory principle is discovered, there is a
tendency to apply it in inappropriate situations. Image processing as used
in this chapter applies *only* to what in the older neurological literature
was called sensory-motor functioning. The more cognitive aspects of brain
function in which the intrinsic (association) systems are implicated are
served by what is now usually referred to as information processing. But
even here a distinction can be drawn between the functions of the poste-
rior and the frontal intrinsic (association) mechanisms. As will be shown,
only the posterior convexity of the brain truly serves as an information
processor. The frontal cortex is involved in computing familiarities from
episodic variations of more or less regularly recurring organism-environ-
ment relationships. These computations were shown dependent on the
operation of peripheral visceroautonomic mechanisms and the participa-
tion of the limbic forebrain.

Data will be reviewed that demonstrate that the posterior convexity
of cerebral cortex is involved in the sampling of alternatives (invariant
properties of a relationship between organism and environment), whereas
the frontal cortex regulates behavior (e.g., habituation to repetitious epi-
sodes) that establishes a familiar context within which information can
then be processed. Let me detail a representative experiment.

A modified Wisconsin General Testing Apparatus (Harlow, 1942) is
used to test 12 rhesus monkeys on a complex problem. The monkeys are
divided into three groups, two operated and one control, each containing
four animals. The animals in one operated group had received bilateral
cortical resections in the posterior intrinsic cortex and those in the other

operated group, bilateral cortical resections in the frontal intrinsic cortex about 2.5 years prior to the onset of the experiment; those in the control group are unoperated. In the testing situation these animals are confronted initially with two junk objects placed over two holes (on a board containing 12 holes in all) with a peanut under one of the objects. An opaque screen is lowered between the monkey and the object as soon as the monkey has displaced one of the objects from its hole (a trial). When the screen is lowered, separating the monkey from the 12-hole board, the objects are moved (according to a random number table) to two different holes on the board. The screen is then raised and the animal is again confronted with the problem. The peanut remains under the same object until the animal finds the peanut five consecutive times (criterion). After a monkey reaches criterion performance, the peanut is shifted to the second object and testing continues (discrimination reversal). After an animal again reaches criterion performance, a third object is added. Each of the three objects in turn becomes the positive cue: testing proceeds as before —the screen separates the animal from the 12-hole board, the objects are placed randomly over 3 out of the 12 holes (with a peanut concealed under one of the objects), the screen is raised, the animal allowed to pick an object (one response per trial), the screen is lowered, and the objects moved to different holes. The testing continues in this fashion until the animal reaches criterion performance with each of the objects positive in turn. Then a fourth object is added and the entire procedure repeated. As the animal progresses, the number of objects is increased serially through a total of 12 (Figure 21.1). The testing procedure is the same for all animals throughout the experiment; however, the order of the introduction of objects is balanced—the order being the same for only one monkey in each group.

Analysis of the problem posed by this experiment indicates that solution is facilitated when a monkey attains two strategies: (*a*) during search, moving, on successive trials, each of the objects until the peanut is found; (*b*) after search, selecting, on successive trials, the object under which the peanut had been found on the preceding trial. During a portion of the experiment, searching is restricted for animals with posterior intrinsic sector ablations; and selection of the object under which the peanut had been found on the previous trial is impaired by frontal intrinsic sector ablations. The effects of the posterior intrinsic sector lesions will be dealt with first.

Figure 21.2 graphs the averages of repetitive search errors by each group. The deficit of the frontally operated group is not associated with search (a result that is discussed later). In spite of the increasing complexity of the succeeding situations, the curves appear little different from those previously reported to describe the formation of a discrimination in complex situations (Bush & Mosteller, 1951; Skinner, 1938). Although one
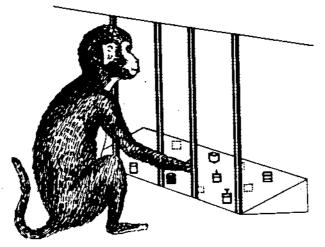
Figure 21.1. Diagram of the multiple object problem showing an example of the seven object situation. Food wells are indicated by dotted squares, each of which is assigned a number. The placement of each object over a food well was shifted from trial to trial according to a random number table. A record was kept of the object moved by the monkey on each trial, only one move being allowed per trial. Trials were separated by lowering an opaque screen to hide, from the monkey, the objects as they were positioned.
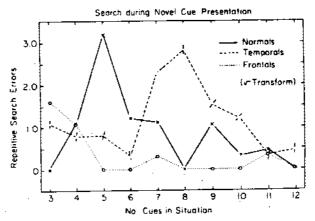

Figure 21.2. Graph of the average of the number of repetitive errors made in the multiple object experiment during those search trials in each situation when the additional, that is, the novel, cue is first added.

might, a priori, expect the number of repetitive responses to increase
monotonically as a function of the number of objects in the situation,
this does not happen. Rather, during one or another phase of the discrimi-
nation, the number of such responses increases to a peak and then declines
to some asymptotic level (Bush & Mosteller, 1951; Skinner, 1938).

Analysis of the data of this experiment has shown that these peaks or
"humps" can be attributed to the performance of the control and poste-
riorly operated groups during the initial trials given in any particular
(e.g., 2, 3, 4 . . . cue) situation, that is, when the monkey encounters a
novel object. The period during which the novel and familiar objects are
confused is reflected in the "hump." The importance of experience as a
determinant of the discriminability of objects has been emphasized by
Lawrence (1949, 1950). His formulation of the "acquired distinctiveness"
of cues is applicable here. In a progressively more complex situation, suf-
ficient familiarity with *all* of the objects must be acquired before a novel
object is sufficiently distinctive to be readily differentiated.

However, there is a difference between the control and the posteriorly
operated groups as to when the confusion between novel and familiar
objects occurs. The peak in errors for the posteriorly operated group lags
behind that of the controls—a result that forced attention because of the
paradoxically "better performance" of the posteriorly operated group
throughout the five to six cue situations (in an experiment that was origi-
nally undertaken to demonstrate a relation between the number of objects
in the situation and the discrimination "deficit" previously shown by this
group).

These paradoxical results are accounted for by a formal treatment
based on mathematical learning theory: On successive trials the monkeys
had to "learn" which of the objects now covered the peanut and which
objects did not. At the same time they had to "unlearn," that is, extin-
guish what they had previously learned—under which object the peanut
had been and under which objects it had not been. Both neural and
formal models have been invoked to explain the results obtained in such
complex discrimination situations. Skinner (1938) postulated a process of
neural induction to account for the peaks in errors, much as Sherrington
had postulated "successive spinal induction" to account for the augmenta-
tion of a crossed extension reflex by precurrent antagonistic reflexes (such as
the flexion reflex). Several of Skinner's pupils (Estes, 1950; Green, 1958) have
developed formal models. These models are based on the idea that both
"learning" (or "conditioning") and "unlearning" (or "extinction") involve
antagonistic response classes—that in both conditioning and extinction
there occurs a transfer of response probabilities between response classes.
This conception is, of course, similar to Sherrington's *"this* reflex or *that*
reflex but not the two together." The resulting equations that constitute
the model contain a constant that is defined as the probability of sampling

a particular stimulus element (Green, 1958), that is, object, in the dis-
crimination experiment presented here. This constant is further defined
(Estes) as the ratio between the number of stimulus elements sampled and
the total number of such elements that could possibly be sampled. This
definition of the constant postulates that it is dependent for its determi-
nation upon both environmental and organismic factors. According to the
model the rapidity of increase in errors in a discrimination series depends
on this sampling ratio—the fewer objects sampled, the more delayed the
peak in recorded errors. The paradox that for a portion of the experiment
the posteriorly lesioned group performs better than the control group
stems from the relative delay in the peak of the recorded errors of the
operated group. The model predicts, therefore, that this operated group
has sampled fewer objects during the early portions of the experiment.
This prediction is tested as shown in Figure 21.3.

The prediction is confirmed. The posterior intrinsic sector is thus
established as one of the organismic variables that determine the constant
of the model. As postulated by the model, the ratio of objects sampled
turns out to be more basic than the number of objects in the situation,
per se.

Returning to the postsearch portion of the multiple object experiment,
Figure 21.4 portrays performance following completion of search, that is,
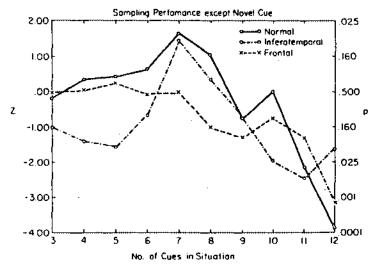after the first response on which the peanut is found. Note that the lag

Figure 21.3. *Graph of the average of the percent of the total number of objects
(cues) that are sampled by each of the groups in each of the situations. To sample, a
monkey had to move an object until the content or lack of content of the food well was
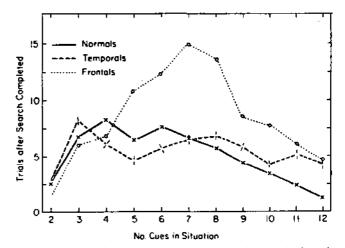clearly visible to the experimenter.*

Figure 21.4. Graph of the average of the number of trials to criterion taken in the multiple object experiments by each of the groups in each of the situations after search was completed, that is, after the first correct response.

shown by the frontally operated group in reducing the number of trials taken to reach the criterion of five consecutive errorless responses (or the number of repetitive errors made) occurs *after* the peanut has been found. This group of monkeys experiences difficulty in attaining the strategy of returning on successive trials to the object under which they have, on the previous trial, found the peanut. Whatever may be the explanation of this difficulty, a precise description can be given: For the frontally operated group, "finding the peanut" does not determine subsequent behavior to the extent that "finding the peanut" determines the subsequent behavior of the normal group. In Sherrington's and in behavioristic terms, the "positive element," the response to the object, is for the frontal group inadequately reinforced by the "alliance with it" of the action, that is, finding the peanut. More generally, response probabilities of the frontal group are less affected by the outcomes of their actions (e.g., finding a peanut).

Interestingly, before the frontally operated group begins to attain the necessary strategy (after the seven cue situation), performance of this group reflects the number of alternatives in the situation. This finding suggests a parallel with analyses of the effects of outcomes developed in the theory of games and economic behavior. The effects of outcome are determined by two classes of variables: (*a*) the dispositions of the organism and (*b*) an estimate about the actions of other parts of the system. The finding that performance of the frontally operated group is related to the number of alternatives in the situation suggests that this group is deficient in evaluating the second class of variables, but this is only suggested by these results.

Support for the hypothesis that frontal lesions do not affect the dispositional variables that determine the effect of an outcome of an action comes from the results of another experiment.

In a constant (fixed) interval experiment, 10 rhesus monkeys are tested in an "operant conditioning" (Skinner, 1938) situation that consists of an enclosure in which a lever is available to the monkey. Occasionally, immediately after a depression of the lever, a pellet of food also becomes available to the monkey. The experimenter schedules the occasions on which the action of pressing the lever has the outcome that a food pellet becomes available. In this experiment, these occasions recurred regularly at a constant (fixed) interval of 2 min. The conditioning procedure, as a rule, results in performance curves (scallops) that reflect during the early portions of the interval, a slow rate of response, and during the latter portions an accelerating rate that nears maximum just prior to the end of the interval. All of the monkeys used in this experiment were trained every other day for 2 hr sessions until their performance curves remained stable (as determined by superimposition of records and visual inspection) for at least 10 consecutive hours.

Two experimental conditions were then imposed, one at a time: (a) deprivation of food for 72 and 110 hr; (b) resection of frontal and posterior intrinsic cortex. Food deprivation increases the total rate of response of all animals markedly, but does not alter the proportion of responses made during portions of the interval (Figure 21.5). Resection of the frontal intrinsic sector does not change the total number of responses, but does alter the distribution of responses through the interval—there is a marked decrease in the difference between the proportion of responses made during the various portions of the interval. Monkeys with lesions of the posterior intrinsic sectors and unoperated controls show no such changes (Figure 21.6).

The results of the constant interval experiment support the contention that the effect of an outcome of an action is influenced by variables that can be classified separately. Deprivation influences total rate of response and the frontal lesion, the distribution of that rate. Deprivation variables are akin to those that have in the past been assigned to influence the disposition of the organism. The frontal intrinsic sector lesion appears to influence the monkey's estimates about the situation. This finding is thus in accord with that obtained in the multiple object problem. Both experimental findings can be formally treated by the device of "mathematical expectation" (von Neumann & Morgenstern, 1953, ch. 1). The distribution of response probabilities in the constant interval experiment can be considered a function of the temporal "distance" from the outcome; distribution of response probabilities in the multiple object experiment is a function of the number of objects in the situation. Frontal intrinsic sector lesions interfere with those aspects of behavior that depend on an estima-
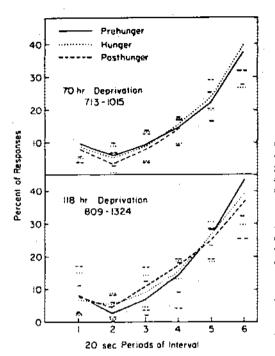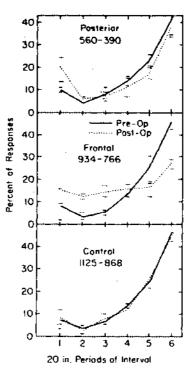
Figure 21.3. *Graph showing the effect of food deprivation on monkeys' rate of lever pressing response to food (a small pellet of laboratory chow) which became available every 2 min. The change in total rate is indicated by numbers under the deprivation label. The lack of change in the distribution responses is shown by the curves. Each curve represents the average of the responses of 10 monkeys; each point represents the average rate during a period of the interval over 10 hr of testing. Variance is indicated by the short horizontal bars.*

tion of the effects that an outcome of an action has in terms of the total set of available possible outcomes. The effects of frontal intrinsic sector lesions on behavior related to outcomes thus parallel the effects of posterior intrinsic sector ablations on behavior related to inputs. A general model of intrinsic sector mechanisms seems therefore to be possible. As a step toward such a model a brief review of available data follows.

The effect of frontal intrinsic sector resection on the distribution of responses in the multiple object and constant interval problems is correlated with other deficiencies in behavior that follow such resections. The most clear-cut deficiency is in the performance of delayed reaction and of alternation by subhuman primates. These problems are usually classified with those used primarily to study behavior involved in the differentiation of alternatives, although differences between the two are recognized. These differences have been conceptualized in terms of one-trial (episode specific) learning (Nissen, Riesen, & Nowles, 1938), immediate memory (Jacobsen, 1936), and retroactive inhibition (Malmo, 1942). More penetrating analyses have been accomplished for the effects of frontal intrinsic sector lesions on the performance of alternation problems (Leary, Harlow, Settlage, & Greenwood, 1952; Mishkin & Pribram, 1956). These analyses emphasize the recurrent regularities that constitute the alternation problems and suggest

Figure 21.6. Graph showing the change in distribution on monkeys' response rate following frontal ablation (three monkeys). Note that the distribution of rate over the interval is not affected in the controls (four monkeys) and after inferotemporal (posterior) ablations (three monkeys). Also note that the total rate of response did not increase; rather rate was somewhat decreased in all groups, probably due to the ad libitum feeding period that all groups were given prior to operation—approximately two weeks before postoperative testing.

that such problems be considered examples of a larger class that can be distinguished from problems that require differentiation (Galanter & Gerstenhaber, 1956). Delayed reaction may also belong to the class of problems specified by episodically recurring regularities: The recurrence, at the time response is permitted, of some of the events present in the predelay situation, constitutes an essential aspect of the delay problem (Mishkin & Pribram, 1956).

These experiments have been followed up by another series that has extended the results to humans and has clearly related the deficit shown by frontally lesioned primates to their inability to compute and control the episode specific variations that occur within the context of regularly recurring variables: (Anderson, Hunt, Vander Stoep, & Pribram, 1976; Brody & Pribram, 1978; Brody, Ungerleider, & Pribram, 1977; Grueninger & Pribram, 1969; Kimble, Bagshaw, & Pribram, 1965; Konow & Pribram, 1970; Luria, Pribram, & Homskaya, 1964; Pribram, Ahumada, Hartog, & Roos, 1964; Pribram & Bagshaw, 1953; Pribram, Plotkin, Anderson, & Leong, 1977; Pribram & Tubbs, 1967; Tubbs, 1969). These studies have shown that the deficit in delayed alternation behavior produced by frontal lesions is due to proactive and retroactive interferences produced by the monotonous tem-

poral context provided by the symmetrical intertrial interval of the classical task, since this deficit can be overcome by imposing a nonsymmetrical delay interval; that interference produced by the continuing distractions involved in manipulating the spatial context in the delayed response task is the critical variable in producing the deficit in performance of this task after frontal resection; that distractibility may be overcome by perseverative behavior under some experimental conditions; and that this continuing distractibility of frontally lesioned human and nonhuman primates is contingent on a failure to produce the viscero-autonomic concomitants of the orienting reaction that accompanies distraction in normal subjects. The results of these experiments demonstrate that the temporal and spatial ordering of behavior and of experience depends on the registration of episode specific occurrences and on composing these registrations into a context in which subsequent behavior becomes appropriate. Such controlled episodic, context-dependent processing can thus be distinguished neurally as well as conceptually from the processing of invariants—true information processing in the Shannonian (Shannon & Weaver, 1949) sense.

Conclusions

This chapter has surveyed data that distinguish three modes of central processing. Image processing was found to occur by virtue of the sensory-motor projection systems of the brain. Evidence was presented that these systems operate as frequency analyzers that operate upon periodicities in energy distributions as transduced by receptor mechanisms. It was further shown that image processing in the frequency domain, by virtue of mathematically described spread functions, distributes input and thus accounts for the distributed nature of the basic memory store.

Image processing is augmented in the primate brain by additional modes of central processing attributable to the functions of intrinsic "association" systems. Evidence was presented to show that the posterior intrinsic systems are involved in information processing, where information is defined as choice among *alternatives*. Choices were shown to depend on sampling a ratio of the number of alternatives available, the size of their ratio being a function of the operations of the posterior intrinsic systems.

By contrast, evidence was presented that showed frontal intrinsic cortex to be involved in controlling behavior dependent on variation in recurrent occurrences (the structure of redundancy in information theoretic terms). Control was shown dependent on computations that registered the "familiarity" among episodic variations in recurrences, in the absence of which every event became "novel" and therefore distracting. Furthermore, registration was shown contingent upon the occurrence of the visceroautonomic components of the orienting reaction.

In short, two modes in addition to image processing were identified. One of these modes depends on differentiating alternatives, the invariances operative in organism–environment relationships that constitute the information upon which knowledge is based. The other mode depends on establishing contextual familiarity from episodes in the variations that characterize recurrent regularities (the structure of redundancy). Delineating these mechanisms of central processing has gone a long way toward dispelling the despair voiced by earlier investigators of brain mechanisms involved in learning and remembering and that for a time turned psychologists away from studies of brain function.

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