Reprinted from: Macromolecules and Behavior. J. Gaito (Ed.) New York: Appleton-Century-Crofts, 1972.

Chapter 17

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Some Dimensions of Remembering: Steps Toward a Neuropsychological Model of Memory

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Interest in the relation of macromolecules to behavior centers on the memory process. It is memory that allows an organism to act on the basis of occurrences removed in time—past and future. It is memory also that allows an organism to act appropriately to present circumstances, for without memory these events constitute nothing more than William James' "buzzing, blooming confusion." The guiding assumption is that this "memory" is effected by macromolecular change in protoplasm, especially in brain tissue. A good part of the search has been for the memory macromolecule; the contents of the present volume attest to the success attained by this approach.

Yet, psychology and neurology and even molecular biology stand to lose much if this continues to be the main approach to the problem. Memory is not of a picce; it is multidimensional. Psychologists have long been aware of the differences between recognition and recall, between long—and short—term memory span, and similar dichotomics. And neurologists have been concerned not only with memory storage but also with the mechanism of retrieval. As a rule, macromolecular processes have been dismissed by these disciplines as important only at the most reductive level—i.e., usually macromolecules have been relegated to the task of longterm storage, *period*. This makes sense only if the sole dimension of memory recognized is that of duration.

There are, however, complexities in the process of remembering which are not easily resolved by this time honored—I am tempted to say hoary —approach. Perhaps the most obvious regards one already mentioned; appropriate reactions to present circumstances. For example, recognition involves not only a memory mechanism of such short duration that it is

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practically instantaneous (How many faces can one recognize in a second?) but also a memory store which is practically unlimited in duration ("You look just the same as when I last saw you—no, it couldn't be twenty years, could it?").

A fresh look at memory seems in order. In the following account I have drawn freely from both old and new knowledge in experimental psychology, neurology, computer and information sciences, as well as from classical molecular biology, for suggestions about the dimensions of remembering and a model of memory. Much of what I have to say is speculative, but the speculation rests solidly on data ordinarily ignored in discussions of memory. The hope is that in this context memory molecules will become properly plural and some of the old pros and cons will give way to new questions for experimentalists.

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Experiencing Experience

Look at a friend, then look at his neighbor, and immediately you experience the difference. In the auditory mode, such transient, rapidly paced recognition—of phrases in music, of phonemic combinations of speech, and so forth—are commonplace. Ordinary views of the memory mechanism have considerable difficulty handling the immediacy, precision and apparent multidimensionality of the evanescent experience. Here a unique process must be in operation. What could it look like; how might it work?

Habit, Habituation, and Awareness

Let me begin by detailing a paradox concerning experience on the one hand and behavior on the other. There are influences on behavior of which we are not aware. In fact, instrumental behavior and awareness are often opposed—the more efficient a performance, the less aware we become. This antagonism is epitomized by Sherrington (1947): "Between reflex action and mind there seems to be actual opposition. Reflex action and mind seem almost mutually exclusive—the more reflex the reflex, the less does mind accompany it." Thus a range of problems is ignored if the focus of inquiry on memory is purely behavioristic.

The reciprocal relationship between experiencing and behavior is perhaps best illuminated by the psychological processes of habit and habituation. If we are repeatedly in the same situation, in an invariant environment, two things happen. One is that if we have consistently to perform a similar task in that environment, the task becomes fairly automatic, i.e., we become more efficient. We say the organism (in this case, ourselves) has learned to perform the task; he has formed *habits* regarding

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it. At the same time the subject habituates, by which we mean that he no longer notices the events constant to this particular task in this environment. His verbal reports of introspection, his failure to move his head and eyes in the direction of the stimulus—electrophysiological measures such as galvanic skin response, plethysmography, and EEG—all attest to the disappearance of orienting with repetition of unvarying input in an unvarying situation. However, habituation is not an indication of some loss of sensitivity on the part of the nervous system but rather the development of a neural model of the environment, an expectancy, a type of memory mechanism against which inputs are constantly matched. The nervous system is thus continually tuned by inputs to process further inputs (Sokolov, 1960).

It is hardly necessary to state that habitual performance of the organism is also due to neural activity. In the case of expectancy there appears to be a diminution of input processing with repetition; in the case of performance, enhanced efficiency of output processing apparently occurs. So the question is: What is the difference between the two kinds of neural activity that makes awareness inversely related to habit and habituation?

Nerve impulses on the one hand, and the slow potentials that occur at synaptic junctions and in dendrites on the other, are available as two kinds of neural processes that could function reciprocally. A simple hypothesis would state that the more efficient the processing of arrival patterns of nerve impulses into departure patterns, the shorter the duration of the design formed by the slow potential junctional microstructure. Once habit and habituation have occurred behavior becomes "reflex." Meanwhile, the more or less persistent designs of slow potential patterns that become constituted are coordinate with awareness. If this view is accepted, it carries with it a corollary, viz., that nerve impulse patterns per se and the behavior they generate are unavailable to immediate awareness. Thus even the production of speech is "unconscious" at the moment the words are spoken. My hypothesis, therefore, is an old fashioned one: that we experience in awareness some of the events going on in the brain but not all.

In short, nerve impulses arriving at junctions generate a slow potential microstructure. The design of this microstructure interacts with that already present by virtue of the spontaneous activity of the nervous system and its previous "experience." The interaction is enhanced by inhibitory processes and the whole procedure produces interference effects. The interference patterns act as analogue crosscorrelation devices to produce new figures from which the patterns of departure of nerve impulses are initiated. The rapidly paced changes in awareness could well reflect the duration of the correlation process.

What evidence is there to suggest that the junctional electrical ac-

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tivities of the central nervous system are involved in awareness? Kamiya (1968) and others have shown, by using instrumental conditioning techniques, that people can readily be taught to discriminate whether their brains are producing alpha rhythms or not, despite the fact that they have difficulty in labeling the difference in the states of awareness they perceive. Subjects who have been able to label alpha rhythm state claim that it is one of pleasantly relaxed awareness. More experiments of this kind are now being carried out in order to find ways to shorten the long educational process currently entailed in Zen, Yogi, and western psychotherapeutic procedures aimed at identifying and achieving pleasant states.

More specific are some recent experiments of Libet's (1966) that have explored a well-known phenomenon. Since the demonstrations in the 1880s by Fritsch and Hitzig (1969) that electrical stimulation of parts of man's brain results in movement, neurosurgeons have explored the brain's entire surface to determine what reactions such stimulations will produce in their patients. For instance, Foerster (1936) mapped regions in the postcentral gyrus which give rise to awareness of one or another part of the body. Thus sensations of tingling, of positioning, etc., can be produced in the absence of any observable changes in the body part experienced by the patient. Libet has shown that the awareness produced by stimulation is not immediate: a minimum of a half second and sometimes a period as long as 5 seconds elapses before the patient experiences anything. It appears that the electrical stimulation must set up some state in the brain tissue and only when that state has been attained does the patient become aware.

The Hologram

But in order for recognition to be effected some more permanent alteration of substrate must act to influence the configuration of arrival patterns. If one looks at EEG records coming off an EEG machine for a number of hours during the day, and then goes home to try to sleep, what happens? The day's records go by in review; but note—they go by *in re*verse. This is known as the "waterfall effect."

Obviously, some neural change has taken place to allow the record to be re-viewed but also obvious is the fact that the re-viewing takes place from a different vantage point than did the original viewing. The record must therefore have "stereo"-like properties that allow it to be examined now from this, now from that, standpoint. This re-viewing from various vantages must not lose its identity relative to the entire record: a familiar face gains, rather than loses, its familiarity and recognizable identity by being viewed from different angles.

The proposal was made above that interactions among the patterns

of excitation which fall on receptor surfaces become, after transmission over pathways organized in a parallel fashion, encoded by virtue of interference patterns of horizontally interacting processes in the slow potential activities of neuronal aggregates to form temporary microstructures whose design is dependent more on the functional organization of neural junctions than on neurons per se as units.

Recently important new advances have been made in the study of interference effects. These advances are the results of a new photographic process which produces images by way of a record called a hologram, which shows some startling similarities to the perceptual process.

Most of us are familiar with the image-generating aspects of physical optical systems. A camera records on photographic film placed at the image plane a copy of the light intensities reflected from the objects within the camera's visual field. Each point on the film stores information which arrives from a corresponding point in the visual field, and thus the film's record "looks like" the visual field. What have been studied more recently are the properties of records made on film which is placed somewhere in front of the image plane on an optical system. When properly exposed by a coherent light source, such a film record constitutes an *optical filter* in which information from each point of the visual field is stored throughout the filter itself. These filters display a number of remarkable characteristics.

As we have all experienced, when a film does not lie exactly in the image plane of a camera, the image becomes blurred, boundaries become less sharp, contrast less marked. In the case of an optical filter, the information is so distributed that there is no resemblance whatever between the stored image and the visual field itself. Thus the optical filter does not visually resemble the original object-rather, it is a record of the wave patterns emitted or reflected from an object. "Such a record can be thought of as 'freezing' of the wave pattern; the pattern remains frozen until such time as one chooses to reactivate the process, whereupon the waves are 'read out' of the recording medium'' (Leith and Upatnieks, 1965). Thus, when transilluminated by a coherent light source, an optical filter reconstructs the wavefronts of light which were present when the exposure was made. As a result, a virtual image of the visual field can be seen by looking towards the filter. This virtual image appears exactly as the visual scene did during the exposure, complete and in three dimensions. In essence, all the information describing the visual field (and from which an image of the visual field can be reconstructed) is contained in the filter.

As the observer changes his viewing position the perspective of the picture changes, just as if the observer were viewing the original scene.

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Parallax effects are evident between near and far objects in the scene: if an object in the foreground lies in front of something else, the observer can move his head and look around the obstructing object, thereby seeing the previously hidden object. . . . In short, the reconstruction has all the visual properties of the original scene and we know of no visual properties of the original scene and we know of no visual test one can make to distinguish the two (Leith and Upatnicks, 1965).

Even before the practical demonstration of the use of optical filters in the reconstruction of images, Gabor (1948; 1949; 1951) had mathematically described another way of producing images from photographic records. Gabor began with the intent of increasing the resolution of electronmicrophotographs. He proposed that a coherent background wave be allowed to interfere with the waves refracted by the tissue. (Reflection from an opaque object would serve as well.) The resulting interference pattern would store both amplitude and spatial phase (neighborhood interaction) information which could then, in a second step, be used to reconstruct, when transilluminated with a coherent light source, an image of the original tissue. Gabor christened his technique holography and the photographic record a hologram because it contains all of the information to reconstruct the whole image.

Gabor holograms can be composed in two ways. A wave form is divided by a beam splitter (e.g., a half-silvered mirror) so that one part can serve as a reference, the other reflected off the object to be photographed. The reference alone can then be used to reconstruct an image. Or, each part of the divided beam can be reflected off a different object. When this is done and one of the objects is used (as a reference) at the time of image reconstruction, the other appears as a "ghost" image. In this instance, the hologram can be used as a mechanism for associative storage of information.

The formal similarity between Gabor's refraction and reflection holograms and the various types of optical filters gradually became evident. The basic similarity between them lies in the fact that the resultant coding of information in each is a linear transformation of the pattern of light not only in terms of the intensity (as in an ordinary photographic process) but also in terms of neighborhood interactions (spatial phase). The most intensively studied holograms have been those in which these phase relationships can be expressed mathematically as Fourier transforms. These equations are a special form of convolutional integrals which have the property that the identical equation convolves and deconvolves. Thus any process represented by the spatial Fourier transform can encode and subsequently decode simply by recurring at some second stage.

Holograms of whatever sort have some interesting properties in common which make them potentially important in understanding brain function. First, the information is replicated and distributed throughout the hologram. This makes the record resistant to damage. Each part of the hologram, no matter how small, can reproduce the entire image; thus the hologram can be broken into small fragments, each of which can be used to construct a complete image. As the pieces become smaller, resolution is lost. On the other hand, as successively larger parts of the hologram are used for reconstruction, the depth of field of the image decreases—i.e., the focus becomes narrowed. Thus an optimum size for a particular use can be ascertained. These curious properties derive from the fact that the hologram is a representation of an image "defocused" in an orderly manner so that information becomes replicated and distributed.

Second, the hologram has a fantastic capacity usefully (i.e., retrievably) to store information. This capacity stems from the fact that when incorporated in a suitable retrieval system, information can be immediately located and accurately reconstructed. The density of information storage is limited only by the wave length of the coherent light and the grain size of the film used. When holograms are produced in solids, many different patterns can be simultaneously stored. Each image is stored throughout the solid, yet each image is individually retrievable. Alternatively,

several images can be superimposed on a single plate on successive exposures, and each image can be recovered without being affected by other images. This is done by using a different spatial-frequency carrier for each picture. . . The gating carriers can be different frequencies . . . and there is still another degree of freedom, that of angle (Leith and Upatnicks, 1965).

At the time of this writing, some ten billion bits have been usefully stored holographically in a cubic centimeter. As Van Heerden and others have pointed out, if we should store during a lifetime as little as one bit per second, the human brain requires approximately 3×10^{10} elementary binary operations *per second*: "If that sort of thing was going on it was incomprehensible . . . However, once confronted with this paradox, it gradually became clear . . . that optical storage and processing of information can provide a way of accomplishing this 'impossible' operation'' (Van Heerden, 1968, pp. 28–29).

A final point about physical holograms. Optical systems are not the only ones that can be subjected to the holographic process. Now that the mathematical relationships have been specified, computer programs have been constructed that "simulate" optical information processes. One such program represents the intensity of an input by the size of a disc; spatial phase relationships are represented by the angular direction of a slit within that disc. Holograms are thus not dependent on the physical presence of

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"waves" even though they are most readily described by the equations of wave mechanics.

This independence of holography from physical wave production is an important consideration in approaching the problem of a neutral holographic process. There is some considerable doubt whether "brain waves" as presently recorded form the substrate of any meaningful interference pattern organization for information processing-although they may be indicative that some such process is taking place. The wave forms recorded for the most part have a long time constant and can therefore be carriers of only very small amounts of information-even in the form of spatially interfering holographic patterns. The hypothesis proposed in the next section, therefore, emphasizes the role of junctional slow-potential microstructures in brain function. These microstructures can be described either in statistical, quantal terms or in the wave-mechanics language of convolutional integrals and Fourier transforms. The microstructures do not change their characteristics because a choice is made as to description. Each language, each descriptive form, has its own advantages. With respect to the problems of perception, especially the questions of image formation and the fantastic capacity of recognition memory, holographic description has no peer. So why not try out its application to brain processes?

A Neural Holographic Process

The essence of the holographic concept is that images are reconstructed when representations in the form of distributed information systems are appropriately engaged. In fact, as noted, one derivative of the holographic process comes from a consideration of optical filtering mechanisms. Holography in this frame of reference is conceived as an instantaneous analogue cross correlation performed by matched filters. In the brain correlation can take place at various levels. In more peripheral stations correlation would occur between successive configurations produced by receptor excitation, the residuals left by adaptation through selfinhibition forming a buffer memory register to be updated by current input. At more central stations correlation would entail a more complex interaction: at any moment input would be correlated not only with the configuration of excitation existing at any locus but also with patterns arriving from other stations.

According to the holographic hypothesis the mechanism of these correlations is not by way of some disembodied "floating field" nor even by disembodied "wave forms." Consider instead the construction of more or less temporary organizations of cortical columns (or in other neural locations, other aggregates of cell assemblies) by the arrival of impulses at neuronal junctions which activate horizontal cell inhibitory interactions.

When such arrival patterns converge from at least two sources their designs would produce interference patterns. Assume that these interference patterns are made up on classical postsynaptic potentials coordinate with awareness, as suggested above. Assume also that this microstructure of slow potentials is correctly delineated by the equations that describe the holographic process, which is also composed of interference patterns. The conclusion would follow that information representing the input is distributed over the entire extent of the neutral pattern just as it is over the entire extent of the physical holographic pattern. This does not mean, of course, that input information becomes distributed willy nilly over the entire depth and surface of the brain. Only those limited regions where reasonably stable junctional designs are initiated by the input, partake of the distribution. Furthermore, for any effect beyond the duration of a particular input more localized enduring memory mechanisms must be invoked. However, these mechanisms can be engaged in loci distributed in neural space once information has become dispersed. Addressing the more permanent store demands merely the repetition of the pattern (or essential parts thereof) which originally initiated storage. This content addressability so readily accomplished by the holographic process does away with the need for keeping track of "where" information is stored.

What are some of the possibilities for making the junctional microstructure endure? Some more lasting property of protoplasm must be invoked to account for storage which can be of varving duration. Profound temporary interactions do occur between inputs separated by hours (as in the McCulloch effect, in which exposures to a set of colored bands influence subsequent observations of color) or in some individuals for days (as in the rare person who shows true eidetic capacities). And, of course, the longer range interactions that account for recognition and recall must also be accounted for. Conformational changes in macromolecules such as lipids or proteins and even longer-lasting anisotropic orderings of macromolecular structure lend themselves to speculation in the following terms. Successive junctional microstructures formed in a region of cortical cytoplasm may produce, when similar in configuration, a cumulative residual effect by inducing ordering into previously disordered macromolecular chains or fibrils, or by increasing an existing order, so that the region thereafter responds more easily to a repetition of the same excitation. Early results of experiments performed on retinal tissue examined with the electronmicroscope show that such changes in molecular conformation can occur with excitation (Sjöstrand, 1969). Similar but as vet unconfirmed suggestions have been made by Whyte (1954) and by Halstead (1951). The former investigation suggests that:

this cumulative medium- and long-range ordering of some of the macromolecular chains throughout a particular volume of cortical cytoplasm

is a kind of growth process of a pattern determined not by heredity but by activity, and involving the development not of a differentiated tissue but of an element of ordering in the molecular arrangement of an extended mass of cytoplasm. Here we are concerned with the differentiation of particular vector directions, possibly parallel to the cortical surface in particular cortical layers. The templates of memory are not single localized molecular structures, but extended components of longrange order set at various angles to one another. . . [However] the ordering will correspond only to the statistically dominant pattern of activity, or simplest overall pattern common to the successive activity patterns. Moreover this tendency to select the dominant pattern will be reinforced by the fact that the simplest overall patterns will be the most stable, since their parts will mutually support one another. The random protein structures may thus act as a structural sieve taking a stable impress at first only of the simplest, most unified, and statistically dominant component in all the patterns of activity of a given general form. In general [then] the development of the modification proceeds from a grossly simplified to a less simplified and more accurate record. This process of the development of a hierarchically organized modification corresponds to Coghill's "progressive individuation" of behavior patterns during ontogeny, and may hold the clue to the self-coordinating capacity of cortical process (Whyte, 1954).

Nor can this be all there is to registering the wave forms. Conformational changes in macromolecules are apt to be reversible. A more permanent record probably demands such mechanisms as the tuning of "averaging circuits" in cortical columns described below and growth induced by the changes in membrane permeability consequent to and dependent on these macromolecular alterations. The "filter," "sieve," or "screen" of holographic patterns is composed not only of the lattice of membrane macromolecules making up the synaptodendritic net but also of a facilitation of all tendencies toward image formation and the initiation of certain departure patterns of nerve impulses.

How then can we approach the problem of changes in protein confirmation as a basis for memory? Sensitization akin to the development of immunities have been proposed. And some initial experimental efforts have been directed toward this view (Mihailović and Janković, 1961). Another lead comes from some incidental observations made during the course of experiments carried out for initially different purposes. In my laboratory we have had occasion to cause epileptic scizures in monkeys by implanting aluminum hydroxide cream in their cortex (Pribram, 1951; Kraft et al., 1960; Stamm and Knight, 1963; Stamm and Pribram, 1960, 1961; Stamm et al., 1958; Stamm and Warren, 1961). Such implantations cause havoe in the learning process. Yet even a major convulsive episode will leave the immediate performance of a learned task unimpaired in these animals. Only 24 to 48 hr *after* such seizures does performance deteriorate—and this in the absence of further seizures. Also, the deterioration is temporary, lasting only about 48 hr. In short: some process takes this many hours to build up sufficiently to challenge the otherwise dominant neural pattern established by learning. And the challenge is temporary; apparently total recrudescence of the learned pattern is reestablished shortly. Organic chemists must have available many macromolecules with similar peculiar characteristics. Are protein conformations subject to such temporary deformations and is the time course of such alterations consonant with that observed in these experiments?

ARRANCING MEMORIES

As I have already indicated, there are many memory processes in which permanent and impermanent features mingle in a variety of ways: memorization of telephone numbers in a strange city, the use of experience in a related-but-novel situation, the schedules which guide us through our daily tasks and pleasures, and the recrudescence of extinguished performances when the conditions of extinction are lifted. These all are memory processes in which more or less temporary arrangements are produced by more permanently stored mechanisms.

Memory and Circuitry

Does the suggestion of a protein conformation mechanism for memory storage dispose, then, of the "neural" or "synaptic growth," or "strengthening" hypothesis? Not necessarily. As I pointed out on another occasion (Pribram, 1963), the electroconvulsive shock experiments have provided evidence that consolidation of the memory trace is at least a twofold process. Immediately after an experience—or 5 sec afterwards, or even up to 1 hr afterwards—all traces of the experience can be wiped out. This suggests, as already noted, that the protein conformation change mechanism is disruptible during this period. After this, more permanent changes gradually take place. But concomitant with the protein conformation change, alterations in the design of the neural circuitry must also take place. Otherwise, retrieval through the generation of appropriate arrival patterns becomes impossible.

Thus another aspect of brain function needs to be called into account: namely, some change in neural connectivity that accompanies the protein changes. A problem arises here mainly because the brain's nerve cells do not divide. However, they can grow new branches. This has been dramatically demonstrated in a study (Rose et al., 1961) of the effects on brain of high-energy radiations produced by a cyclotron. Remarkably minute and sharply demarcated laminar destruction (often limited to a single cell layer, and this is not necessarily the most superficial one) were produced in rabbit cerebral cortex when high-energy beams were stopped short by the soft tissue. The course of destruction and restitution was then studied histologically. Intact nerve cells were seen to send branches into the injured area; these branches became progressively more organized until, from all that could be observed through a microscope or measured electrically, the tissue had been repaired.

The organization of the branches of nerve cells could well be guided by the glia that pervasively surround these branches. Such directive influences are known to be essential, for example, in the regeneration of peripheral nerves. Schwann cells, close relatives of glia, form a column into which the budding fibers must grow if they are not to get tangled in a matted mess of their own making.

The operative assumption is that glial cell division is somehow spurred by those same activities recounted above as being important to memory storage. Data to support this assumption are presented below. The resulting patterns of the glial bed would form the matrix into which nerve cell fiber growth occurs. Thus guided, fiber growth is directed by its own excitation-with the whole mechanism based, however, on the longlasting intervention of glia. This "arranging" mechanism would account for the later "interfering" effects obtained in the consolidation experiments and in the spontaneous "restitution" as well. The growing nerve cell fiber is ameboid and can temporarily retract its tip, which is made up of a helical winding of small globular protein molecules. After the convulsive "insult" is over, first tentative, and then more vigorous probings are found to be resumed in some "random-walk" fashion by the nerve fiber tip (as has been suggested regarding normal growth by von Foerster, 1948). The glial substrate, assumed to be undamaged in this experiment, will perform its guiding function to effect the apparent restitution. Support for the glially guided "growth" hypothesis comes from the work of Krech et al. (1960). These investigators found that the cerebral cortex of rats actually becomes thicker as a function of experience-thickening of visual cortex with visual experience and of somatic cortex with somatic experience were demonstrated. The increased cortical volume was not due to an increase in the number of neurons; rather, glia and fibers were responsible for the change.

The glially guided neural growth hypothesis, in addition to accounting for the late-interference effect data, has another attractive feature. The electrochemical memory storage process per se has no built-in mechanism which satisfactorily explains retrieval. A neural network structured through growth glially guided by experience could, on the other hand, serve retrieval much as do the "feelers" on the magnetic memory core of a comG,

puter. The patterns of electrical signals that activate particular network configurations would then correspond to the lists or programs fed to a computer, as well as to the schemata proposed by Bartlett (1961) to account for the results of his studies on memory in man.

Dismembering and Remembering

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According to the view developed thus far, inputs are both isomorphically recorded as protein conformation changes and coded into programs through neural growth. These programs, when properly activated, reconstruct the appropriate protein conformation, i.e., the "memories." Three observations in addition to the facts of recognition given carlier support the isomorphic recording of input items. One is the occurrence of eidetic imagery; another is the phenomenon of hypnotic regression (Gebhard, 1961); and a final one is the evocation of "memories" by electrical brain stimulation. There are limitations to all of them. The evidence for verisimilitude in hypnotic regression has been questioned. Evocation of "memories" by electrical brain stimulation occurs only in epileptic (i.e., scarred) cortex and is subject to influences of environmental set (Mahl et al., 1962). The occurrence of eidetic imagery in the adult is extremely rare and—curiously, considering the interest such a phenomenon must arouse in psychologists-studies on eidetics are relatively few (e.g., Haber and Haber, 1964; Haber, 1969; Luria, 1968; Stromeyer, 1970). The evidence is thus overwhelmingly in favor of the suggestion that, in addition to some memory storage record, memory processing depends heavily on programs. Bartlett (1961) amply documented the view that schemata are stored in the head.

In many ways this clarifies the memory problem considerably. If storage were only isomorphic to experience, one should be able to locate and find direct correspondences between all of the stored items and the world "out there." In a schematic or programmed memory no such isomorphic relation would have to obtain. The difference is essentially that between, say, a dictionary and a typewriter, between a trigonometry table in a handbook of physics and chemistry and a calculating machine. For example, if I take a simple adding machine and add to it the capability to multiply, I am putting a new memory mechanism into it. If I look into the machine I will find a change and that change may be the addition of a set of registers. Yet I will never find any specific "product" by opening the machine. "Products" are obtained when the machine is presented with inputs which "signal" that a product is required, inputs anisomorphic to the "products" themselves. This seems self-evident and is often forgotten in our more erudite arguments about memory.

Much confusion would be resolved if we adhered to the notiondeceptively simple, yet immensely significant-that "remembering" is the

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opposite of "dismembering." Even our language reflects that remembering is a putting together, a reconstruction. Once accepted, the conclusion this leads to is remarkable; namely, it means that a good deal of what we call the memory storage problem is a hoax. Most "memory" is stored in our libraries and in our jobs and homes as inputs to our brain machines. The human organism is thus signaled to remember what he is programmed to remember. The very word "remember," as I have suggested, reflects this process of reconstruction from parts as by a machine. A word of caution is appropriate at this point, however; in no sense do I want to imply that man is "nothing but a machine." Man as often as not goes to the library in search of the appropriate signals; he plans and controls, as often as not, the significant—i.e., signifying—aspects of his home and job. The point is that, in these respects as well as in the assembly of appropriate routines and programs, remembering is an active, not a passive process.

The Numbers Game

Once we dispose of the hoax that isomorphic coding and recording of all inputs is the sole necessity for a "proper" memory mechanism, we can also get rid of the "numbers game" that is constantly being played when memory is discussed. Bits of information are thus seen as irrelevancies—every book an author writes can be "stored" in his typewriter, which possesses fewer than 50 symbols on its registers. One can raise the objection that the brain must be more complicated than a typewriter—and I agree; but the number of states that it can register involves an experimental rather than a logical or psychological debate. An alphabet of only 26 letters does an heroic job.

I have repeated these things, which by now are almost truisms, because I find that in our discussions and our literature we do not hold these facts in mind. Over and over, the argument revolves only around storage of particulars. There need not be 10^{10} units for storage; there need not be an RNA change specific to a Y maze but not to a T maze. The rules of the numbers game hold only if one elects to play it. Only if the model one holds is one based *exclusively* on item storage—the storage of inputs in some isomorphic manner—is this kind of argument valid. And the evidence is overwhelming that there is more to memory than bit-by-bit storage.

Hierarchy

Implicit, then, is the idea that our memory machinery is capable of hierarchical organization-that all small units and probably some larger combinations of the memory machinery are permanent and undamageable, but that at least some of the larger units can be flexibly combined through programming operations initiated either by the input or by even larger permanent units. Also implicit is the suggestion that a particular memory unit or state can serve in a variety of combinations and thus participate in the production of a variety of re-membrances.

"Hierarchy" here implies several things: first, on any occasion I know all-of-a-piece whether I have anything at all relevant in memory to express; second, the mechanics of expression demand that I produce only one memory at a time. This limitation on output is the "keystone in the construction of the individual," as Sherrington (1947) so beautifully stated it. Thus serial ordering accomplished by an hierarchy of processes prior to output is yet another dimension essential to remembering (see, e.g., Hart, 1965).

A sophisticated statement by Werner (1969)-based in part on his own extensive research and that of Hartline et al. (1956), of Mountcastle et al. (1963), Poggio and Mountcastle (1960), and of Hubel and Wiesel (1968), and in part on computer programming formulations presented by Miller et al. (1960)-describes a process for somesthetic perception which applies with only minor modifications to the other input systems. Werner discerns a basic columnar structure in the brain cortex in which each neuron of the column displays a receptive field which "is the finest indivisible unit" of representation of the input. Columns of neurons tend to display identical or at least similar receptive fields and thus make up one level of representation. Columns are in turn combined into more complex structures by directionally sensitive units which serve as pointers connecting the activities of the columns. These pointers, depending on the preferred direction of response, structure the electrical activities of the columns into various relationships to one another; if pointers with more than one direction are available, blocks of columns become connected to form "ring structures." Werner compares his cortical columnar structures to the list structures out of which computer programs are constructed. Each list contains items that point to other lists. Thus complex interactions (list structures) can be programmed by this simple device. In fact, Spinelli (1970) has designed a program (called Occam) to stimulate a feature analyzer based on this cortical structure. This program can be tuned by the presentation of patterns of nerve impulses or wave forms to respond subsequently when certain features of the wave form are repeated.

A somewhat simplified version of Werner's and of Spinelli's feature analyzer is composed as follows. A cortical column is conceived to consist of input and operator neurons, and of interneurons and test cells. An input to a neural unit of the column that displays a receptive field is distributed to interneurons which in turn connect to an operator neuron. The interneurons are tunable—i.e., they adapt and habituate; they have memory. Each interneuron thus acts as does a bin in a computer that averages the patterns of input to which it is exposed. Only when a pattern is repeated does structured summation occur—nonrepetitive patterns simply raise the baseline and average out. Thus the operator neuron, sensitive solely to *patterns* of excitation, is activated only when input patterns are repeated. The entire process is sharpened by feeding the output from the operator neuron back onto the input cell via a test neuron that compares the pattern of neural activity in the input and operator neurons. When match is adequate, the test cell produces an exit signal, otherwise the tuning process continues. Thus each cortical column comes to constirute an engram by virtue of its specific sensitivity to one pattern of neural activity, a "list" of interresponse times of a firing neuron or the wave form that describes the envelope of the firing pattern.

Each cortical column is conceived of as being connected with others via horizontal cells and their basal dendrites which are responsible for inhibitory interactions. Whenever these horizontal cells are activated in an unsymmetrical fashion, as they are by directional sensitive inputs, a temporary structure constructed of several columns is put together. These extended structures, dependent as they are on hyperpolarization rather than on nerve impulse transmission, are composed therefore by processes taking place at neural junctions and constitute temporary neural states.

We now have good evidence that the so-called association areas of the cerebral cortex exert control over the input systems, control which is in many respects similar to that exercised when a zoom lens is extended and retracted (Pribram, 1969). This function would have the effect of changing the number (and perhaps the complexity) of cortical columns that can be contained in a temporary structure.

The logic of the input systems can thus be conceived constituting a feature filter on input, a screen that is being continually tuned by that input. One of the characteristics of the filter is, therefore, that it constitutes a self-adapting system whose parameters of adaptation are controlled by its own past history and by the operations performed on it by other neural mechanisms.

The Temporal Code

This flexible rearrangement of hierarchically organized memories demands that some important attribute of neuronal function is sufficiently flexible to be temporarily but effectively alterable. This attribute might well be the temporal code with which the nerve discharges, or to which it is sensitive (see, e.g., Hydén, 1961; Landauer, 1964).

Direct experimental evidence for any such flexibility in the temporal

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code with which neurons fire has hitherto been sparse. Almost the sole evidence that the brain is at all capable of altering its rhythms as a function of experience comes from the pioneering studies of John and Killam (1959). These investigators flashed light to their subject at certain frequencies (e.g., 30/sec) and recorded from various locations in the brain.

In brief, their experiments demonstrate that at the beginning of training the electrical activity of a wide variety of brain structures appears to be synchronous with a repetitive stimulus. After learning has occurred and performance is at criterion, the electrical activity synchronous with the stimulus can be recorded only from the appropriate projection system. In the earlier phases of learning, the electrical activity of many of the core areas of the brain stem and forebrain show such synchrony: the reticular formation, hippocampus, and amygdala are only a few of the structures involved. The synchronous rhythms drop out progressively and the dropping out is correlated with progressively better performance on the part of the animal.

An additional observation which may point the way toward which future efforts for evidence of temporal coding may be directed comes from my laboratory (Spinelli and Pribram, unpublished data). Small wire electrodes were implanted in the lateral geniculate body and in the striate cortex of monkeys. Those in the geniculate were so placed that electrical stimulation would encompass a large portion of the entire nucleus, and continuous stimulation with 5-volt biphasic pulses, occurring at approximately 8/sec, was applied. Bipolar recordings were made from the cortical electrode placements. Most of them reflected more or less accurately the rhythm of stimulation imposed on the geniculate station of the visual system. From some of the cortical placements, however, arrythmic recordings were consistently obtained; they sounded like a complex tap dance when transduced by a loudspeaker. The brain cortex apparently has a remarkable power to alter a rhythm imposed at an adjacent station.

The Temporal Hold

The above-noted observation leads us immediately to the question: How, then, are rearrangements among temporal codes accomplished? As yet no biological mechanism has been proposed to effect flexibility; nor will I attempt to propose one in detail here. But the imposition of local D.C. potentials on brain tissue is effective not only in altering the firing pattern of nerve cells but also in maintaining---i.e., temporarily storing--this change (Chow, 1964; Chow and Dewson, 1964; Dewson et al., 1964).

Further, lesions of the limbic forebrain and of the anterior frontal isocortex impair just the type of task which demands the flexible rearrangement of memory processes. I have elsewhere (Pribram et al., 1964) suggested that this deficit is due to a failure of the regulation of the "temporal hold" imposed by an input on a particular matrix of registers. This "temporal hold" is assumed to be accomplished through an operation similar to that which gives rise to a temporary dominant focus in the experiments of Ukhtomski (1962), Rusinov (1956), and Morrell (1961). Without regulation by such a hold mechanism, the organism fluctuates inordinately among possible temporal codes and thus produces only a jumble of arrival patterns. In such circumstances even the temporary conditions necessary to the registration of interference patterns as holograms cannot be achieved. Support for some sort of temporal hold process emanating from the frontolimbic portions of the brain comes from electrical recordings made in man:

When conditional and imperative stimuli are presented in this way a remarkable change appears in the frontal brain response; a negative potential appears immediately after the conditional response and endures until the imperative response, when it declines rapidly to zero or becomes positive. This has been described as the "Contingent-Negative Variation" or Expectancy Wave (Walter, et al., 1964). In conditions such as those described, the E-wave is the most constant and stable of all electro-cerebral phenomena in normal adults. It does not depend on the character of the intrinsic normal rhythms and is as large and extensive with the eyes open as shut. In children, however, and in mentally disturbed patients, the E-wave is often elusive and variable; above all, it is extremely sensitive to social influences.

As already mentioned the E-wave arises always and only during sensory-motor association, but both the sensation and the motion may be of quite a subtle nature. In the simplest case the presentation of a conditioned stimulus in any modality, followed by an imperative stimulus in another modality, evokes an E-wave following the primary conditional responses and lasting until the moment when the imperative response would have occurred.

The striking feature of the E-wave is that it appears, as it were, to submerge the imperative response, and terminates very abruptly at the instant when the latter would have subsided. The typical sawtooth waveform of this phenomenon is remarkably like that of the time-base of an oscilloscope, rising steadily toward a maximum value over a time determined by the established stimulus interval, and dropping suddenly to zero. The duration of the E-wave as studied systematically so far is several seconds, but in some subjects the potential difference seems to be sustained much longer during "extinction" trials when there is no imperative stimulus to act as a "fly-back" trigger. Sometimes there is even a suggestion of a staircase or "Treppen" effect when conditional stimuli are presented at intervals of a few seconds without reinforcement to subjects with a very slow rate of extinction. Since the E-wave presumably represents depolarization of the apical dendritic plexus, the possibility of "recruitment" in such a mechanism would be interesting to study in more detail. The subjects who have shown signs of this effect are highly suggestible and easily hypnotized (Black and Walter, 1963); the capacity to maintain a high and even cumulative level of expectancy may be typical of this disposition, and may depend on some idiosyncrasy of the electrochemical relations in the superficial cortical levels (Walter, 1964).

And so we are back to the problem of matching temporary changes in protein conformation against some more lasting arrangement of memory structures so that, on occasion, some permanent neural organization can be achieved.

RNA AND REINFORCEMENT

RNA and Behavior

Despite the difficulty in ridding ourselves of conceptual shackles, progress is being made by leaps and bounds. Hydén's work has often been criticized by both psychologists and biochemists; yet the picture he began to draw for us is nevertheless taking form. The RNA changes he reports may indeed be occurring—but not necessarily as evidence of item storage on evanescent messenger molecules, but rather as evidence of derepression of genomes. Bonner's theory (see Chapter 16, present volume) and Hvdén's (1961) evidence are in accord.

But greater difficulties are posed by such phenomena as cannibalism and the injection of "knowledgeable" RNA. Here is a focus of discrepancy —here is the point where experimentation must take the offensive and attack. The evidence must be firmed-up; new directions must be taken to decipher the relationship. But, again, the problem comes into better focus if RNA is not considered the memory molecule. Rather, the question might be put: Just what is the relation between RNA and derepression? An increase in RNA can signal to the experimenter merely that derepression has occurred. Could it also be that RNA in some way can initiate i.e., induce—derepression? There is good evidence from embryology that this may actually be so. The process of induction in the embryo has many similarities to the process of reinforcement which establishes the memory trace in the adult.

Inductors in Review

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In essence, induction is a "chemical conversation"—as Bonner has called it—between the intrinsic determining mechanisms of the morphogenetic field (or its already-independent differentiated parts) and the extrinsic organizing properties which guide its flowering. An early experiment, the classic example, is that of the determination of the lens by the eye vesicle. Contact between this vesicle with the overlying epidermis stimulates the latter to form a lens in the region of contact. If the eye vesicle is removed the epidermis fails to differentiate a lens. This experiment raised a whole set of problems which generated a direction of research in experimental embryology bearing a striking resemblance to current explorations in experimental psychology and ethology (see, e.g., Hamburger and Levi-Montalcini, 1950).

The first and logical assumption was that the inductor acted merely as a trigger; that, in the classical example, the head skin is already "predisposed" to form a lens and that it requires only a signal to start. Two lines of evidence disproved this concept of induction. First, the optic vesicle was shown by transplantation to induce a lens in skin other than head skin—for example, flank skin. Second, the area of head skin which normally forms a lens was shown by other transplantation experiments to be *polypotential* and therefore definitely not "predetermined" for lens formation only. If the region of the head epidermis which normally forms the lens is combined with an ear induction, for example, it will respond with ear formation; if combined with a nose inductor, it will form a nose.

These facts do not deny, however, that the reacting system must be "ready" or "competent," i.e., in the proper state of responsiveness, to allow induction to become effective. For example, tissue which is already "launched," as it were, toward a different destination, will fail entirely to respond.

Another point is that inductors are not species-specific. An inductor can be effective on tissues which belong to a different species, genus, or even order. The suggestion is, therefore, that inductors are made up of chemicals common to many organisms (more of this in a moment). These chemicals apparently determine the overall character of the induced structure while the hereditary equipment of the cells of this structure determines its detailed form. For example, when the flank skin of a frog embryo was induced to form head structures by salamander tissue into which it was transplanted, the embryo had a salamander head with the horny jaws and other features of the frog.

A long series of chemical experiments has currently culminated in the view that the ribonucleic acids (RNAs) are most likely, and perhaps uniquely responsible for the inductive effect (see Niu, 1959), though ribonucleoproteins and steroids have not been entirely ruled out. For the most part RNAase destroys the inductive effect, although the problem remains that RNAase has other effects on the induced tissue which may disrupt its differentiation. More direct evidence, however, comes from demonstrations of the inductive effect of RNA extracted from different organs. Not only has this been accomplished, but RNA isolated from

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different sources was shown to be capable of inducing the recipient tissue to differentiate into different specific structures. These experiments suggest that there are *many* species of RNA in an organism and that each has a specific function.

With the use of ¹⁴C-labeled RNA, another problem has been tackled. Evidence has been established to show that it is possible for RNA molecules actually to move from the microsomes of the inductor tissue into the cells of the tissue induced, most likely by a process of pinocytos's.

To sum up: embryogenesis is dependent not only on the inherited and inherent properties of the genetic constitution of the organism; rather, these properties are also evoked and organized by the inductive capacity of the milieu in which the cells grow. The inductive capacity is itself specific, but in a somewhat different sense than is the genetic potential. The genetic capability is individual-, species- (and genus- and order-) specific. Hereditary factors proscribe commonalities with the past and future while assuring variation within any single generation. Inductors, on the other hand, are nonspecific with respect to individuals, species, and so forth. They are relatively simple chemicals—RNAs—common to all living organisms. Inductors thus provide the existential commonality which allows the possibility of modification of whole generations according to the exigencies of the time.

Induction and Reinforcement

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The superficial descriptive similarity between induction as studied in embryological tissue and reinforcement as studied in conditioning situations is easily drawn. (1) Inductors evoke and organize the genetic potential of the organism. Reinforcers evoke and organize the behavioral capacities of organisms. (2) Inductors are relatively specific as to the character they evoke but are generally nonspecific relative to individuals and tissues. Reinforcers are relatively specific in the behaviors they condition but are generally nonspecific relative to individuals and tasks. (3) Inductors determine the broad outlines of the induced character; details are specified by the action of the substrate. Reinforcers determine the solution of the problem set; details of the behavioral repertoire used to achieve the solution are idiosyncratic to the organism. (4) Inductors do not just trigger development; they are more than just evanescent stimuli. (5) Inductors must be in contact with their substrate in order to be effective. Contiguity is a demonstrated requirement for reinforcement to take place. (6) Mere contact, though necessary, is insufficient to produce an inductive effect; the induced tissue must be ready, must be competent to react. Mere contiguity, though necessary, is insufficient to produce reinforcement; shaping, deprivation, readiness, context, expectation, attention, hypothesis—these are only some of the terms used to describe the factors which comprise the competence of the organism without which reinforcement cannot become effective. (7) Induction usually proceeds by a two-way interaction—or, as stated earlier, by way of a chemical conversation. Reinforcement is most effective in the operant situation where the consequences of the organism's own actions are utilized as the guides to its subsequent behavior.

But when this much has been said, the question still remains as to whether these descriptive similarities point to homologous mechanisms. My hypothesis states that they do. What evidence is there in support? What neural processes become operative during conditioning?

What is required is an anatomical pathway that functions at multiple locations in the brain to release the reinforcing "inductor," the chemical that can induce the recipient tissue to differentiate. Ketv (1970) in a provocative synthesis of recent neurochemical research, makes the following suggestion. Scheibel and Scheibel (1967) have described a system of neurons (some of which lie in the brain-stem reticular formation) which function as nonspecific afferents to the cerebral cortex. The axons of these cells are characteristically long and at their terminations produce climbing fibers which twine around the apical dendrites of pyramidal cells with a loose axodendritic coupling in contrast to the well defined synapses that characterize specific afferents. Fuxe et al. (1968) claim to have shown that the nonspecific couplings are largely aminergic, that the axons and their cells of origin contain nor-epinephrine. The local release of norepinephrine can be responsible for instigating the induction process by stimulating the secretion of RNA and facilitating protein synthesis. Evidence is accumulating that cyclic adenine monophosphate may be the mediator of this process. Kety remarks that "it is interesting that the stimulation of protein kinase by cyclic adenine monophosphate can be markedly potentiated by magnesium or potassium ions and inhibited by calcium which suggests means whereby an effect of adrenergic stimulation could be differentially exerted on recently active and inactive synapses."

But such experiments tell us only that certain neural processes are possibly equivalent to those set up when reinforcement is manipulated extrinsically. Somewhat closer to demonstrating the mechanism with which we are concerned are experiments in which a temporary dominant focus is produced in the brain. The classical example is the chemical stimulation of the exposed motor cortex of a dog that has been conditioned to lift his left forepaw. When strychnine is placed on the cortical area that controls the right hind limb, the dog will lift the right hind limb instead of the left forepaw when given the usual signal. Once the chemical is removed, the dog reverts to its former behavior unless the stimulation has been often repeated. It is plausible to conclude that fieldlike configurations of such temporary dominant foci as these are produced during conditioning and the function to organize subsequent neural, and therefore behavioral, activity. But this, although relevant, is another story and has already been alluded to.

A more chronic and therefore more easily studied change in neural discharge can be obtained by making epileptogenic lesions in cortex with implantations of aluminum hydroxide cream or by locally freezing the cortical tissue.

In my laboratory different areas of the brain cortex of monkeys have been treated with aluminum hydroxide cream to produce local irritations manifested by altered electrical activity (abnormal slow waves and spike discharges). Such irritative lesions, while they do not interfere with a monkey's capacity to remember the solution to problems repeatedly solved prior to the irritation, do slow their original learning of these problems some fivefold (Henry and Pribram, 1954, Kraft et al., 1960; Pribram, 1951; Stamm et al., 1958; Stamm and Pribram, 1960, 1961; Stamm and Warren, 1961). Moreover, problem-solving in general is not affected; the defect is specific for those solutions to tasks which cannot be remembered when that particular part of the brain has been removed. Furthermore, the impairment is restricted to the early part of the learning process, the part before there is actual demonstration that learning is occurring. Thus the irritative lesions do not block consolidation but do delay its manifestation. Could it be that a single engram restricted to one neural locus is insufficient to be manifest? There is a good deal of evidence from human learning experiments that considerable rehearsal must take place in order that an experience be remembered (Trabasso and Bower, 1968). What appears to occur during rehearsal is a distribution of the rehearsed material so that it becomes linked to a larger assortment of previously stored experience. The results of the irritative lesion experiments can thus be interpreted as showing that the process of reduplication and distribution of the engram has been retarded. A test of this interpretation would come from a comparison of learning by irritative-lesioned monkeys under spaced and massed trial conditions.

Histological analysis of the tissue treated with aluminum hydroxide shows tangles of nerve fibers much as those described in peripheral nerves when growth is not properly guided by an adequate Schwann cell column. Could it be that oligodendroglia are selectively killed off by the treatment, allowing the disordered growth to occur? Chemical analysis of the tissue implanted with aluminum hydroxide cream is, of course, impractical. But an ingenious experiment designed to answer this question has been achieved (Morrell, 1960). An irritative lesion made in one cerebral hemisphere produces, after some months, a "mirror focus" of altered electrical activity in the contralateral cortex by way of the interhemi-

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spheric connections through the corpus callosum. This "mirror focus" has not been directly damaged chemically, yet it possesses all of the epileptogenic properties of the irritative lesion. The RNA in this mirror focus has been shown to be considerably altered when compared to that found in normal brain tissue. Once more, RNA production by nerve cells has become involved in experiments undertaken to study the memory mechanism.

Thus there is every reason to believe memory induction, just as embryological induction, to be a multistage process which takes time to run off. Each stage in such a process would be expected to show its own vulnerabilities, vulnerabilities that can be demonstrated by appropriate techniques applied at the critical period. We have learned much about critical periods in embryogenesis and behavior development. A rich field of exploration and experimentation lies ahead in determining the nature of critical, i.e., sensitive, periods in mnemogenesis.

CONCLUSION

The thoughts expressed in this chapter have centered on the process we call remembering, but the interwoven complexities of the psychological mechanism have led me into a discussion of awareness, of temporal coding in the nervous system, of the "holding" functions I attribute to the frontal and limbic forebrain, and of a molecular mechanism of reinforcement. I have not given all of the evidence available in support of the proposals made, nor have I given evidence to jeopardize the views presented. I have chosen this course deliberately-for, aside from pressing the fruitful course of laboratory exploration now in progress-I feel a great need to re-view and restructure my image of the problem. I fear that the present views of the memory problem will soon-or perhaps already have begun to-lead prematurely to a dead end and thereby permit the experimental challenge to wither away unanswered. Already I am tired of hearing that RNA really doesn't have anything to do with learning-i.e., not real learning -because it has not been known to store the "association" necessary to learning. And how many times have we seen the memory problem reduced to information storage? I can image as many bits of succulent and poignant detail about a loved one as you will give me time and an interested ear. And in my imagination I can do this while possessing the routine of my daily affairs, with hardly a perceptible effect on my behavior. Just where are the questions about "short-term," "intermediate," and "long-term" memory processes leading? Are there more types than these (e.g., very, very short), or are we dealing with a continuum? So goes the argument, which unfortunately misses the point that memory has structure; that in order to process nonsense syllables, man must know language; that to "forget" the irrelevant, the relevant must be properly available.

This need to restructure my thinking has thus produced this chapter and the classification used here, the division of memory mechanisms into "evanescent," "arranging," and "rein-forcing" processes which I believe to be pertinent to a range of problems in biology and psychology. In it *novelties* are emphasized at the expense of tried truths: the neural hologram, rearrangements among neural configurations, an aminergic-RNAmechanism of reinforcement by induction. Here are some new possibilities which may finally enable us to realize that memory mechanisms are no more monolithic in their structure than are macromolecules.

Acknowledgments

The author thanks Dr. Walter Tubbs for editorial assistance, and the United States Public Health Service for Research Career Award MH 15,214 which made the present manuscript possible.

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