34 BRAIN SYSTEMS AND COGNITIVE LEARNING PROCESSES

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I. BEYOND ASSOCIATION

Experimental analyses of the learning process have developed into two rather different approaches. One, carried out by biologically oriented scientists, seeks to establish the locus of plasticity, and the nature of the more or less permanent changes which allow an accumulation of experience to alter behavior. The other engages computer-oriented scientists and experimental psychologists using human subjects. It focuses on the nature of processes of retrieval: Questions are asked regarding the span which can handle a store, the types of accessing which make available that which is stored, and the structures of the accessing processes. Both of these approaches are based on a model in which the memory store associates spatio-temporally contiguous experiences and accumulates the residues of such associations which then become accessible when some similar experience addresses the storage locus.

This associative model, while valuable in the analyses of simpler forms of learning such as classical and instrumental (operant) conditioning, may not encompass problems encountered when the learning of cognitive processes is involved. Nor does the associative model, as it is currently conceived, allow for the likely possibility that the memory mechanisms of the brain are content rather than location addressable.

A content addressable cognitive learning process involves coding the residues of experience in such a way that subsequent experience automatically addresses the residue on the basis of similarity rather than on the basis of location. Whereas a location addressable process traverses the same paths during acquisition and retrieval, a content addressable process operates somewhat more independently of specific pathways. Mailing a letter uses a location-addressable mechanism; broadcasting a television program utilizes a degenerate form of content addressability (the content is encoded on a carrier frequency).

The work reported here suggests that the cognitive operations of the primate brain are essentially coding operations which "label" the residues of experience so as to make them readily retrievable. In such a scheme, classification of learning processes ought, at some level, to mirror the classification of retrieval mechanisms. Thus, the evidence from experiments involving the primate forebrain, which makes up the bulk of this chapter, should overlap and be congruent with that obtained from the approaches used in memory research involving humans. But at the same

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time a more comprehensive understanding of the role of the primate forebrain in learning should be achieved.

The primate brain is a complex organ composed of many systems and subsystems. Damage to one system influences some learning but not all; damage to another system will affect learning processes considerably different from those influenced by injury to the first. Even when consideration is restricted to work in my laboratory, a variety of types of learning can be distinguished: the learning of perceptual or motor skills, reference learning, learning based on interest, and learning to transfer experience gained in one situational context to another. This leaves out higher-order forms of learning such as linguistic learning which in its fully-developed form is uniquely human.

In this chapter, I shall develop evidence which suggests that these varieties of cognitive learning processes can be arranged hierarchically according to the brain systems which have been identified to be involved. The specifics of the hierarchy proposed will most likely be subject to change as new evidence accrues. However, I will maintain that the complexities of cognitive learning processes will not be understood until the relationships among them and to brain systems becomes clarified. The current tendency to do no more than to serve up series of dichotomies results only in a monumental tower of Babel.

At least seven different learning processes can be identified. At the base of the hierarchy, shown in Figure 34.0, there are four processes that form two basic branches. In the first are the perceptual and motor skills, and in the second, the processing of interesting or novel (registration) and familiar (extinction) episodes. Skills are elaborated by search and sampling procedures to form the next higher level: the *referential* learning processes. Episodic learning, dependent on registration and extinction, becomes elaborated by spatio-temporal probability structures which at a higher level, frames the *context* within which the episodes occur, and allows transfer of the training obtained in one context to another. In turn, referential and contextual learning processes interact to produce declarative linguistic learning.

Each of the nodes of the hierarchy has a forebrain system identified with it. Thus perceptual learning involves the primary sensory systems; motor learning, the primary motor systems. Processing novelty involves systems converging on the amygdala; processing the familiar involves those converging on the hippocampus. (See also Chapter 33, by Gray, this volume.) Search and sampling are disturbed by resection of the posterior intrinsic, probabilistic programming by resections of the far frontal cortex. The methods and data from which these conclusions stem are described below.

II. THE MULTIPLE DISSOCIATION TECHNIQUE

The experimental analysis of subhuman primate model systems has uncovered a host of learning disturbances. The initial method by which these brain-behavior relationships were established is called the method of multiple dissociation based on an "intercept of sums" technique (Pribram,

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                          Declarative
                          Linguistic


              Contextual                    Referential


    Spatiotemporal   Episodic        Automatic        Search and
    Probability                      Skill            Sampling
    [FarFrontal]                                      Procedures
                                                      [Posterior Intrinsic]


         Registration  Extinction    Motor    Perceptual
         [Amygdala]    [Hippocampus]  [Motor]  [Sensory]
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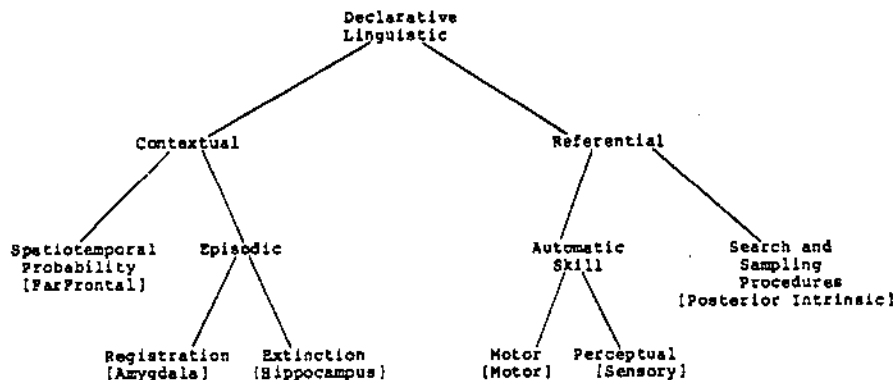
FIG. 34.0.   Hierarchical scheme of relationships between types of cognitive learning based on their involvement with particular cerebral systems.

1954) akin to what Teuber named the method of double dissociation of signs of brain trauma in humans. The multiple dissociation technique depends on classifying the behavioral deficit produced by cortical ablations into yes and no instances on the basis of some arbitrarily chosen criterion; then plotting on a brain map the total extent of tissue associated with each of the categories *ablated: deficit; not ablated: no deficit;* and finally finding the intercept of those two areas (essentially subtracting the *noes* from the *yesses-plus-noes.*) This procedure is repeated for each type of behavior. The resulting map of localization of disturbances is then validated by making lesions restricted to the site determined by the intercept method and showing that the maximal behavioral deficit is obtained by the restricted lesion. (See Table 34.0 and Figure 34.2)

Once the neurobehavioral correlation has been established by the multiple dissociation technique, two additional experimental steps are undertaken. First, holding the lesion constant, a series of variations is made of the task on which performance was found defective. These experimental manipulations determine the limits over which the brain-behavior disturbance correlations hold and thus allow reasonable constructions of models of the learning and retrieval processes impaired by the various surgical procedures.

Second, neuroanatomical and electrophysiological techniques are engaged to work out the relationships between the brain areas under examination and the rest of the nervous system. These experimental

TABLE 34.1
Simultaneous Visual Choice Reaction

		Operates without deficit				Operates with deficit			Nonoperate controls	
		Pre	Post			Pre	Post		Pre	Post
OP	1	200	0	PTO	1	120	272	C 1	790	80
OP	2	220	0	PTO	2	325	F	C 2	230	20
OP	3	380	0	PTO	3	180	F	C 3	750	20
LT	1	390	180	PTO	4	120	450	C 4	440	0
LT	2	300	350	T	1	940	F		•	
H	1	210	220	T	2	330	F			
HA		350	240	VTH	1	320	F			
FT	1	580	50	VTH	2	370	F			
FT	3	50	0	VTH	3	280	F			
FT	4	205	0	VTH	4	440	F			
FT	5	300	200	VT	1	240	F			
FT	6	250	100	VT	2	200	F			
DL	1	160	140	VT	3	200	890			
DL	2	540	150	VT	4	410	F			
DL	3	300	240	VT	5	210	F			
DL	4	120	100							
MV	1	110	0							
MV	2	150	10							
MV	3	290	130							
MV	4	230	10							
MV	5	280	120							
CIN	1	120	80							
CIN	2	400	60							
CIN	3	115	74							
CIN	4	240	140							

Note-- Pre- and post-operative scores on a simultaneous visual choice reaction of the animals whose brains are diagrammed in Figure 34.2, indicating the number of trials taken to reach a criterion of 90% correct on 100 consecutive trials. Deficit is defined as a larger number of trials taken in the "retention" test than in original learning. (The misplacement of the score H 1 does not change the overall results as given in the text.)

procedures allow the construction of reasonable models of the functions of the areas and of the mechanisms of impairment.
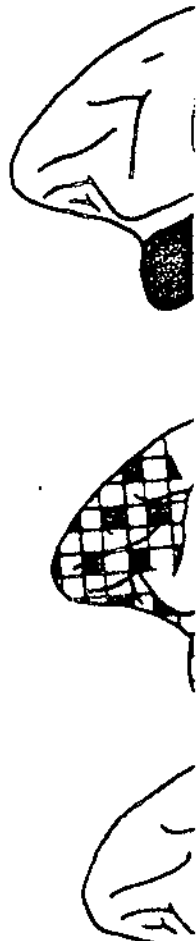
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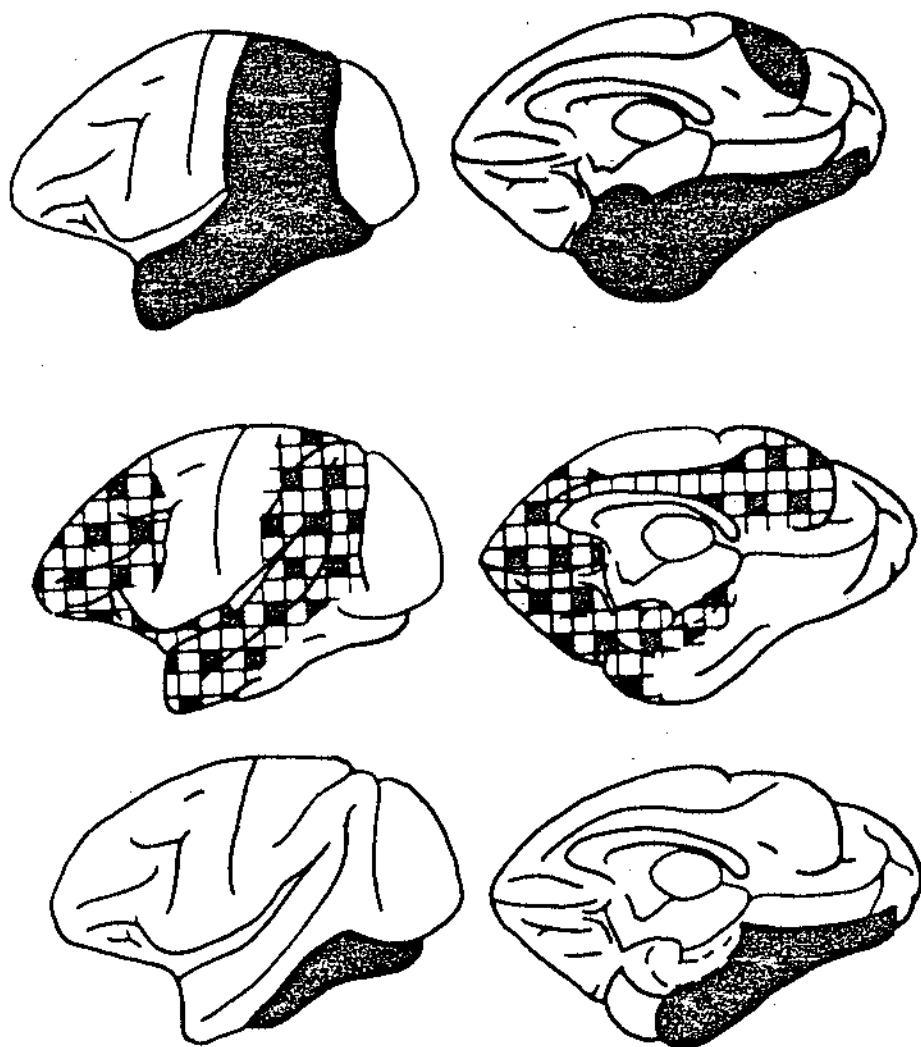rese
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FIG. 34.2. The upper diagram represents the sum of the areas of resection of all of the animals grouped as showing deficit. The middle diagram represents the sum of the areas of resection of all to the animals grouped as showing no deficit. The lower diagram represents the intercept of the area shown in the black in the upper diagram and that not checkerboarded in the middle diagram. This intercept represents the area invariably implicated in visual choice behavior in these experiments.

III. PERCEPTUAL AND MOTOR SKILLS

A. PERCEPTUAL LEARNING

The impetus for work in our laboratory to study perceptual learning came from studies by Patrick Bateson, an ethologist at Cambridge University. In his thesis, Bateson (1964, see 1972) had shown that imprinting is a special case of perceptual learning. He raised newborn chicks in an environment of either horizontal or vertical stripes, and showed that this early experience dramatically influenced subsequent imprinting. Thus, it appeared that the development of an expectancy or neuronal model was as important to imprinting as to later perceptual performances (as shown by Sokolov, 1960). Once the model was established, learning took place within one or at most a very few trials. Bateson then showed, at Stanford, that a similar type of nonproblem-oriented (latent) learning occurred in young monkeys.   A pattern was placed in the animals' home cage for three months.   Then a discrimination task was given using this pattern in connection with a novel one and learning was compared to that obtained in a task where the novel one was matched to one which had previously been used in a problem solving situation. The "latently"-learned cue proved easily as influential in determining behavior as did the "problem" learned one.

Direct evidence from brain recordings also confirms the fact that perceptual learning can proceed without help from problem-guided learning. Records of the electrical activity evoked in the occipital (striate) cortex of monkeys shows a differentiation of wave forms even when the animal is simply exposed to two different patterns (Spinelli, 1967) and before discrimination learning has taken place (Pribram, Spinelli, & Kamback, 1967).

Sharpening of the difference in wave forms occurs over the course of several repeated exposures to the patterns. Furthermore, the cortical electrical responses either increment or decrement (Grandstaff & Pribram, 1972; Bridgeman, 1982) and the sites for these differential responses are distributed.   After the initial incrementing or decrementing, which occurs over the first five or so trials, each specific electrode placement provides consistent and reliable recordings which continue unchanged from day-to-day and week-to-week.   Adjacent placements show markedly different electrical response patterns, that is, the spatial arrangement of these cells appears to be random.   We concluded, therefore, that at the cortex a configuration develops during perceptual learning and that perception is a function of this configuration.

Considerations which I have reviewed elsewhere (Pribram, 1966; 1969; 1974; 1982), have led me to propose that this configuration resembles a quantally organized multiplexed (strip or patch) holographic pattern.   The critical evidence is the fact that extensive destructions of primary projection cortex do not interfere with pattern recognition except for the production of scotomata (i.e., holes in the sensory field).   The mechanism upon which recognition is based must therefore be distributed over the primary cortex and perceptual recognition must therefore result from an operation which constructs or composes it by means of the distributed

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mechanism. Direct neuroelectric evidence for such distribution comes from the experiments just cited. The concept of a neural hologram, that is, of sets of interfering wave forms (or of a matrix of hyper- and depolarizations) constituted of postsynaptic and dendritic potentials, provides a reasonable model that handles many hitherto unexplainable neurobehavioral data and provides a solid base for the associative properties of recognition. These data include the lack of effect of epileptogenic lesions and cortical cross hatchings on perceptual performances (Kraft, Obrist, & Pribram, 1960; Stamm & Pribram, 1961; Stamm & Knight, 1963; Stamm, Pribram, & Obrist, 1958; Stamm & Warren, 1961; Pribram, Blehert, & Spinelli, 1966; Sperry, Miner, & Meyers, 1955; for review, see Pribram, 1982, Chapter 6). The reconstructive process is, however, complicated and will be reviewed in the section on Reference Learning.

B. MOTOR LEARNING

Our experiments on the nature of motor learning were motivated by the question posed in the neurological literature as to whether muscles or movements are represented in the motor cortex. In an experiment which was designed to replicate a study of Lashley's (1929), we found (Pribram, Kruger, Robinson, & Berman, 1955) that resection of large extents of motor cortex did not produce weakness of any muscle group, nor did the resection interfere with any specific movement (defined as a sequence of muscle contractions and studied by examining progressive frames of cinematographic records obtained in different behavioral situations). What we did find was a marked delay in acquisition, and a change in the fluency of performance in opening a latch box and retrieving a peanut (reaction times doubled or tripled). Since no such change in reaction times was seen in other practiced situations, I interpreted the change in performance to indicate that a specific problem-solving act had been impaired. Thus, it appeared that the issue of representation was even more complex than had been stated. Not only muscles but movements and actions (defined as the consequences of movements) had to be considered. The resolution of the problem came when it was realized that the representation of muscles was anatomically determined, the representation of movements resulted from physiologically-oriented studies, while the concept of a representation of actions came from neurobehavioral experimentation. All three types of representation were, in fact, tenable: the issue is not which, but how the representations interact. Other ways of stating the problem are: How (by what physiological process) are the anatomical organizations which characterize the motor system mapped into the behaviors of the organism? How do movements relate muscles to the environment upon which they operate?

A clue to how such mappings might occur came from the work of Bernstein (1965) in which he made cinematographic analyses of the actions of humans performing tasks such as hammering nails, jogging on a spring-supported platform, or writing on a blackboard. His subjects were dressed in black leotards but had white spots marking their joints. The photographic film therefore recorded the movements of the joints as the

actions were carried out. The record consisted of a pattern of continuous waveforms, one for each joint. By performing a frequency analysis on the waveforms, Bernstein was able to correctly predict the amplitudes and locations of the next movements in the sequence.

It seemed plausible to me that the analyses which served Bernstein so well might similarly serve the motor systems of the brain, especially as there is considerable evidence (noted above) that the sensory systems operate by way of such waveform analytic processes. We therefore undertook some experiments to determine whether single neurons in the basal ganglia and cerebral motor cortex were frequency selective. The results of the experiment showed that a 20% portion of a total of 308 cells sampled resonate (i.e., increase or decrease their activity at least 25% over baseline spontaneous activity) to a narrow (1/2 octave) band of the range of cycle frequencies.

Tuning could be due to a spurious convergence of factors relating to the basic properties of muscle as discussed in the introduction: metric displacement and tonicity or tension. An examination was therefore undertaken of variables related to these basic properties, variables such as velocity, change in velocity (acceleration), as well as tension, and change in tension. These factors in isolation were found not to account for the frequency selective effects. This does not mean that other cells in the motor system are not selectively sensitive to velocity and tension. But it does mean that the frequency selectivity of the cells described is dependent on some higher order computation of the metric and tonic resultants imposed by the foreleg musculature and by the external load.

The other variable investigated was position in the cycle of movement. Position *is* encoded by cortical cells (and not by caudate nucleus cells) but only at the site of phase shift and only for a particular frequency. The result thus supports the hypothesis that the cortical cells are in fact frequency selective, in that any sensitivity to phase shift presupposes an encoding of phase and therefore frequency. Furthermore, the fact that the cortical cells respond to position suggests that they are directly involved in the computation of the vector space coordinates within which actions are achieved.

There is thus no question but that an approach to analysis of the functions of the motor system in frequency terms is useful not only in studying the overall behavior of the organism, but in studying the *neural* motor mechanisms involved in the acquisition of motor skills. Motor learning, just like perceptual learning, appears to depend on computations involving the networks of the primary sensory and motor cortexes, computations which are readily carried out in the frequency domain but which can be specified as well in terms of quantal matrix characteristics.

C. AUTOMATIC (SKILLED) VERSUS CONTROLLED (PROCEDURAL) PROCESSING

There is additional evidence that, for some tasks at least, learning needs only the primary projection, input-output systems of the brain. Shiffrin and Schneider (1977; Schneider and Shiffrin, 1977) and Treisman (1977) have developed tasks which differentiate between automatic and

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controlled processing. They differ in that tasks which can be automatically processed involve over-learned skills in which a choice can proceed without serial search. Thus, the number of alternatives from which a cue is chosen has no effect on reaction time since all are processed in parallel. Controlled processing involves an earlier stage of skill and requires a serial search with reaction time dependent on the number of alternatives.

To determine what brain systems were involved in these two types of reference learning tasks, we used a modification of Treisman's displays and measured the event-related electrical activity recorded from the striate and peristriate cortex, the inferior temporal lobe, far frontal and precentral cortex of monkeys. The subject had to select a green square from a set of a colored squares and diamonds, each of equal contour and luminance when compared to the rewarded cue.

The following display combinations were used in the experiment described here: a) a simple disjunctive display in which the green square had to be identified in a background of eight red diamonds; b) a more complicated disjunctive display in which the green square had to be identified in a background of red diamonds, white circles, and blue triangles not held identical); c) the conjunctive display in which the green square had to be identified in a background of green diamonds, red diamonds and red squares. The results showed that differences in the electrical recordings made from the primary sensory areas reflected differences in distinct features of the displays. Conversely, changes in potentials recorded from the posterior intrinsic association cortex reflected the difficulty of the task as determined by the number of alternatives and the conjunctive/disjunctive dimension. When the task was novel, the far frontal intrinsic cortex was shown also to be involved.

Other experiments have allowed us to make a dissociation between the brain electrical activity evoked in the primary sensory projection cortex and the posterior intrinsic association cortex of the temporal lobe (Rothblat & Pribram, 1972; Nuwer & Pribram, 1979). These earlier studies, as well as the current ones, showed that the brain electrical activity evoked in the primary sensory receiving areas was largely determined by the features in the stimulus display, irrespective of whether they were being reinforced, whereas the electrical potential changes evoked in the temporal cortex were primarily related to the cognitive operations, i.e., the choices involving categorizing or pigeon holing (Broadbent, 1974). Clear and consistent involvement of the frontal cortex was found only on occasions when the task was novel or the reinforcing contingencies were shifted between runs. These relationships to categorizing and novelty are consonant with the results described below.

IV. REFERENCE LEARNING AND THE POSTERIOR CORTICAL CONVEXITY

A. SENSORY SPECIFICITY

Between the sensory projection areas of the primate cerebral mantle lies a vast expanse of parieto-temporo-preoccipital cortex. Clinical observation has assigned disturbance of many cognitive and language functions to lesions of this expanse. Experimental psychosurgical analysis in subhuman primates of course, is limited to nonverbal behavior; within this limitation, however, a set of sensory-specific agnosias (losses in the capacity to categorize cues) have been produced. Distinct regions of primate cortex have been shown to be involved in each of the modality-specific cognitive functions: anterior temporal in gustation (Bagshaw & Pribram, 1953), inferior temporal in vision (Mishkin & Pribram, 1954) midtemporal in audition (Weiskrantz & Mishkin, 1958; Dewson, Pribram, & Lynch, 1969) and occipitoparietal in somesthesis (Pribram & Barry, 1956; Wilson, 1955). In each instance, categories learned prior to surgical interference are lost to the subject postoperatively and great difficulty (using a "savings" criterion) in reacquisition is experienced, if task solution is possible at all.

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

B. SEARCH AND SAMPLING PROCEDURES

All sorts of differences in the physical dimensions of the stimulus, for example, size, are processed less well after inferior-temporal lesions (Mishkin & Pribram, 1954) but the disability is more complex than it at first appears — as illustrated in the following story:

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

To test this hypothesis, monkeys were trained in a Ganzfeld made of a translucent light fixture large enough so the animal could be physically inserted into it (Ettlinger, 1957). The animal could press a lever throughout

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the procedure but was rewarded only during the period when illumination was markedly increased for several seconds at a time.   Soon response frequency became maximal during this "bright" period.   Under such conditions no differences in performance were obtained between infero-temporally lesioned and control animals.   The result tended to support the view that if an infero-temporally lesioned monkey did not have to make a choice he would show no deficit in behavior, since in another experiment (Mishkin & Hall, 1955) the monkeys failed to choose between differences in brightness.

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

This result gave further support to the idea that the problem for the operated monkeys was not so much in "seeing" but in being able to *refer* in a useful or meaningful way to what had been reinforced previously. Not only the stimulus conditions but an entire range of response determinants appeared to be involved in specifying the deficit.   To test this more quantitatively, I next asked whether the deficit would vary as a function of the *number of alternatives* in the situation (Pribram, 1959).   It was expected that an informational measure of the deficit could be obtained, but something very different appeared when I plotted the number of errors against the number of alternatives (see Figure 34.3).

If one plots repetitive errors made before the subject finds a peanut – that is, the number of times a monkey searches the same cue – *vs.* the number of alternatives in the situation, one finds there is a hump in the curve, a stage where control subjects make many repetitive errors.   The monkeys do learn the appropriate strategy, however, and go on to complete the task with facility.   What intrigued me was that during this stage the monkeys with infero-temporal lesions were doing better than the controls!   This seemed a paradox.   However, as the test continued, the controls no longer made so many errors, whereas the lesioned subjects began to accumulate errors at a greater rate than shown earlier by the controls.

When a stimulus sampling model was applied to the analysis of the data, a difference in sampling was found (Figure 34.4).   The monkeys with infero-temporal lesions showed a lowered sampling ratio; they sampled fewer cues during the first half of the experiment.   Their defect can be characterized as a restriction on the number of alternatives searched and sampled.   Their sampling competence, that is, their competence to process information, had become impaired.   The limited sampling restricted the ability to construct an extensive memory store and to reference that memory during retrieval.

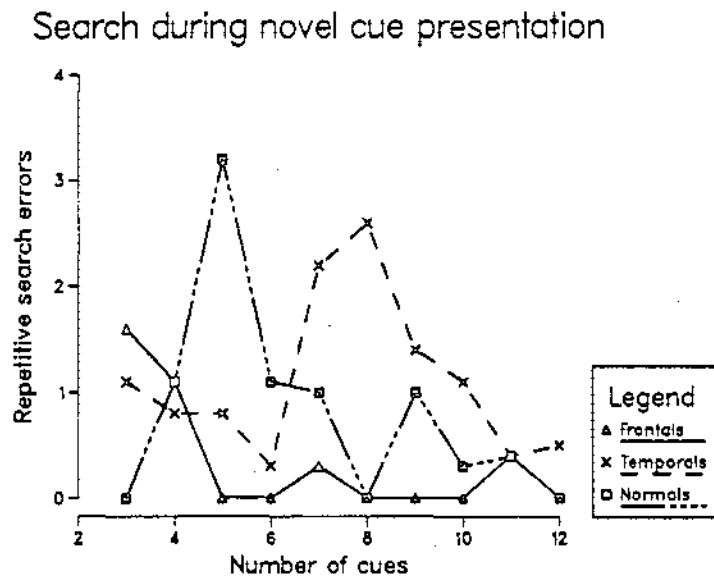## Search during novel cue presentation

FIG. 34.3. The average 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.

C. ELEMENT LEARNING

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

To investigate whether learning proceeds by sampling one element at a time, eight monkeys were trained on a two choice and a five choice sample displayed on the screen of the DADTA panels of which only one was rewarded when pressed. The choices of individual monkeys were plotted for each of the cues sampled by panel pressing. As can be seen from the accompanying figure (Figure 34.5), sampling of cues is initially random, producing prolonged periods of stationarity. Behavior then becomes concentrated on the rewarded cue in steps, each of which is preceded by another period of stationarity and the elimination (i.e., choice
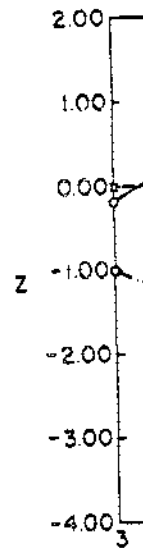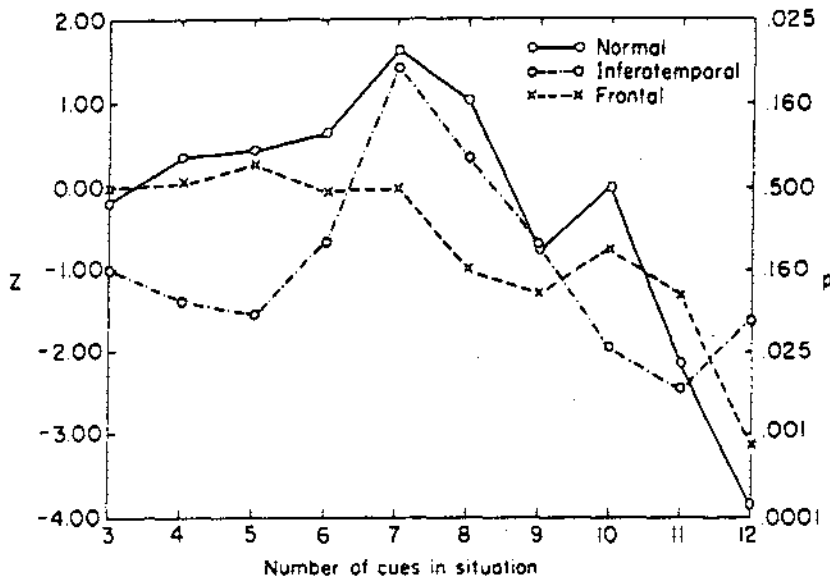
FIG. 34.4. The average proportion of objects (cues) that are sampled (except novel cue) by each of the groups in each of the situations. To sample, a monkey had to move an object until the content or lack of content of the food well was clearly visible to the experimenter. As was predicted, during the first half of the experiment the curve representing the sampling ratio of the posteriorly lesioned group differs significantly from the others.

drops to zero) of one of the unrewarded cues.

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

Subtle effects are obtained, however, when abnormal electrical foci are induced by implanting epileptogenic chemicals in the cortex. In such preparations, the period of stationarity in a two-choice task is increased five-fold. Despite this, the slope of acquisition, once it begins, remains unaffected. Obviously during the period of stationarity something is going on in the nervous system — something which becomes disrupted by the process which produces the electrical abnormality. Perhaps that something devolves on distributing the effects of trial and error over a sufficient reach of the neural net until an adequate associative structure is attained.
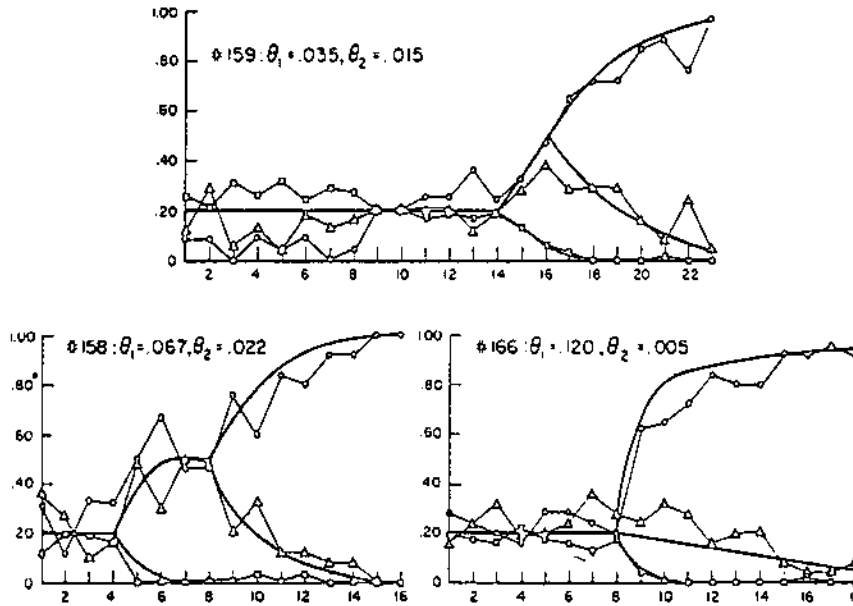
FIG. 34.5. Observed and predicted proportion responses to each stimulus for individual subjects on multiple discrimination in 25-trial blocks. Each curve represents a different stimulus. Solid lines represent predictions based on restricted sampling. The ordinate shows the proportion of responses, the abscissa shows 25-trial blocks.

D. REFERENCE LEARNING

How do the search and sampling systems interact with the perceptual and motor systems to produce skilled performance? We have shown that recovery functions in the primary visual and auditory systems have been influenced by electrical stimulations of the sensory specific intrinsic association areas and the frontolimbic systems (Spinelli & Pribram, 1966).

This influence is a function of the attentive state of the monkey (Gerbrandt, Spinelli, & Pribram, 1970). Visual receptive fields have also been shown to become altered by such stimulation (Spinelli & Pribram, 1967). Finally, the pathways from the sensory specific intrinsic association and frontolimbic formations to the primary input systems have been to some extent delineated (Reitz & Pribram, 1969). Perhaps the most surprising findings of these studies is that input control is to a large measure effected through structures which had hitherto been thought of as regulating motor function.

This brings me to a consideration of the brain as the instrument with which we develop learning skill. The brain as we know it now is considerably different from the one that early learning theorists thought they were working with. Most formulations of learning depended heavily
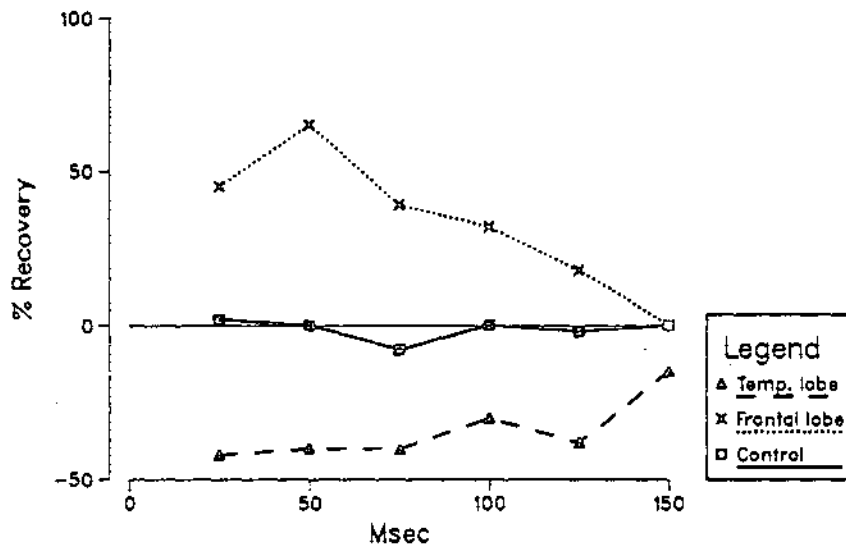
FIG. 34.6. The percentage recovery during stimulation compared to prestimulation response. Control stimulations were performed on the parietal cortex.   Records were made immediately after the onset of stimulation and weekly for several months.   Stimulations one month later showed no significant change. -

on the concept of associative strength based on contiguity and number. Configural variables were relegated to perception and the existance of perceptual learning was, until the past two decades, denied or ignored. Further, the configural and sampling aspects of perceptual learning had not been teased apart.

An even more pervasive difficulty with classical learning theory is its dependence on the reflex-arc, stimulus → organism → response model of brain function. We now know that the brain is organized along servo-mechanism principles. The discovery of the function of the gamma efferent fibers of motor nerves made it necessary to modify our conceptions of the organization of the reflex and therefore of behavior. Thus, sensory functions are controlled by output systems; behavior is regulated not by a piano keyboard control over muscle contraction but by servo-control of the setting of muscle receptors (see Pribram, Sharafat, & Beekman, 1983). In such a brain, learning is hierarchic and constructional: the brain must build up programs to organize perceptions and to compose a behavioral repertoire. Instead of simple "association" by contiguity, learning proceeds by matching configurations; and the accretion of skills through practice (the develoment of subroutines) occurs by dropping out unnecessary actions and movements, not by forming new associative connections.

V.   EPISODIC LEARNING AND THE LIMBIC FOREBRAIN

A. CONTEXTUAL LEARNING

The second major division of the cerebral mantle to which learning functions have been assigned by clinical observation lies on the medial and basal surface of the brain and extends forward to include the poles of the frontal and temporal lobes. This frontolimbic portion of the hemisphere is cytoarchitecturally diverse.   The expectation that different parts might be shown to subserve radically different functions was therefore even greater than that entertained for the more uniform posterior cortex. To some extent this expectation was not fulfilled: Lesions of the frontolimbic region, irrespective of location (dorsolateral frontal, caudate, cingulate-medial frontal, orbitofrontal, temporal polar-amygdala, and hippocampal) disrupted "delayed alternation" behavior.   The alternation task demands that the subject alternate his responses between two cues (for example, between two places or between two objects) on successive trials. On any trial the correct response is dependent on the outcome of the previous response. This suggests that the critical variable which characterizes the task is its temporal organization.   In turn, this leads to the supposition that the disruption of alternation behavior produced by frontolimbic lesions results from an impairment of the process by which the brain achieves its temporal organization.   This supposition is only in part confirmed by further analysis: It has been necessary to impose severe restrictions on what is meant by "temporal organization" and important aspects of spatial organization are also severely impaired.

For instance, *skills* are not affected by frontolimbic lesions, nor are discriminations of melodies. Retrieval of long-held memories also is little affected.   Rather, a large range of short-term memory processes are involved.   These clearly include tasks which demand matching from memory the spatial location of cues (as in the delayed response problem) (Anderson, Hunt, Vander Stoep, & Pribram, 1976) as well as their temporal order of appearance (as in the alternation task) (Pribram, Plotkin, Anderson, & Leong, 1977). A similar deficit is produced when, in choice tasks, shifts in which cue is rewarded are made over successive trials (Mishkin & Delacour, 1975). The deficit appears whenever the organism must fit the present event into a "context" of prior occurrences, and there are no cues which address this context in the situation at hand at the moment of response.

B. THE REGISTRATION OF EVENTS AS EPISODES

As noted, different parts of the frontolimbic complex would, on the basis of their anatomical structure, be expected to function somewhat differently within the category of contextual memory processes. Indeed, different forms of contextual amnesia are produced by different lesions. In order to be experienced as memorable, events must be fitted to context A series of experiments on the orienting reaction to novelty and its registration have pointed to the amygdala as an important locus in the

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"context-fitting" mechanism. The experiments were inspired by results obtained by Sokolov (Sokolov, 1960).

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

The orienting reaction and habituation are thus sensitive measure of the process by which context is organized. We therefore initiated a series of experiments to analyze in detail the neural mechanisms involved in orienting and its habituation. This proved more difficult than we imagined. The dependent variables - behavior, GSR, plethysmogram, and electro-encephalogram - are prone to dissociate (Koepke & Pribram, 1971).

Forehead plethysmography turned out to be especially tricky, and we eventually settled on behavior, the skin conductance (GSR), heart and respiratory responses, and the electrical brain manifestations as most reliable.

The first of these experiments (Schwartzbaum, Wilson, & Morrissette, 1961) indicated that, under certain conditions, removal of the amygdaloid complex can enhance the persistence of locomotor activity in monkeys who would normally decrement their responses. The lesion thus produces a disturbance in the habituation of motor activity (Figure 34.7).

The results of the experiments on the habituation of the GSR component of the orienting reaction (Bagshaw, Kimble, & Pribram, 1965) also indicate clearly that amygdalectomy has an effect (Figure 34.8). The lesion profoundly reduces GSR amplitude in situations where the GSR is a robust indicator of the orienting reaction. Concomitantly, deceleration of heartbeat, change in respiratory rhythm, and some aspects of the EEG indices of orienting also are found to be absent (Bagshaw & Benzies, 1968). As habituation of motor activity (Pribram, 1960a, b) and also habituation of earflicks (Bateson, 1972) had been severely altered by these same lesions, we concluded that the autonomic indicators of orienting are in some way crucial to subsequent behavioral habituation. We identified the process indicated by the autonomic components of the orienting reaction as "registering" the novel event.

However, the registration mechanism is not limited to novelty. Extending the analysis to a classical conditioning situation (Bagshaw & Coppock, 1968; Pribram, Reitz, McNeil, & Spevack, 1979) using the GSR as a measure of conditioning, we found that normal monkeys not only
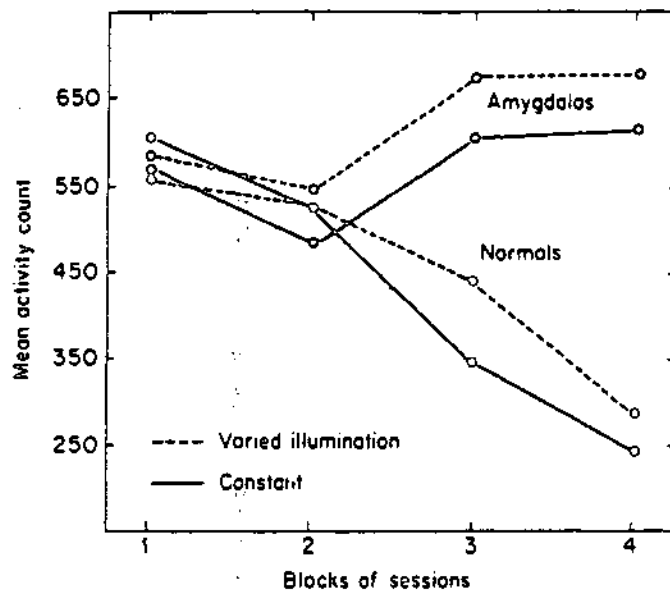
FIG. 34.7. Postoperative activity scores of normal and amygdalectomized
monkeys for successive blocks of three sessions under conditions of
constant illumination and more intense, varied illumination.

condition well but produce earlier and more frequent anticipatory GSR's as
time goes by. Amygdalectomized subjects fail to make such anticipatory
responses. As classical conditioning of a striped muscle proceeded
normally, it is not the conditioning *per se* which is impaired. Rather, it
appears that registration entails some active process akin to rehearsal
– some central mechanism aided by viscero-autonomic processes that
maintains and distributes excitation over time.

Behavioral experiments support this suggestion. Amygdalectomized
monkeys placed in the 2-cue task described above fail to take proper
account of reinforced events. This deficiency is dramatically displayed
whenever punishment, that is, negative reinforcement, is used. For
instance, an early observation showed that baboons with such lesions will
repeatedly (day after day and week after week) put lighted matches in their
mouths despite showing obvious signs of being burned (Fulton, Pribram,
Stevenson, & Wall, 1949). These observations were further quantified in
tasks measuring avoidance of shock (Pribram & Weiskrantz, 1957). The
results of these two experiments have been confirmed in other
laboratories and with other species so often that the hypothesis needed to
be tested that amygdalectomy produces an altered sensitivity to pain.
Bagshaw and Pribram (1968) put this hypothesis to test and showed that
the threshold of GSR to shock is not elevated as it would be if there
were an elevation of the pain threshold. Rather the threshold is, if
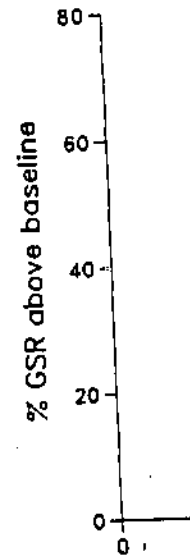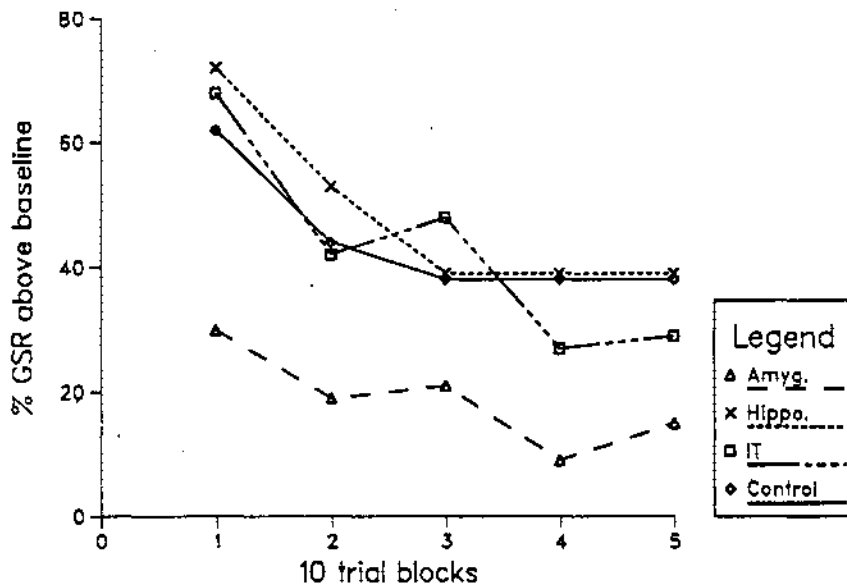anything, reduced by the ablation. This experimental result suggests that

FIG. 34.8. Curves of percent GSR response to the first 50 presentations of the original stimulus for the control and three experimental groups (Hippo., IT, Amyg.), i.e., hippocampal, inferior temporal, and amygdala resected monkeys.

amygdalectomy produces its effects by way of a "loss of fear" defined as a disturbance in "registering" the noxious event by placing it in context. In other words, the animal does not *remember* the noxious event; its recurrence is experienced as novel and not fear-producing.

Another set of data are relevant to this issue of registration. These data were gathered within an entirely different frame of investigation. Around the turn of the century, the observation was made that after severe head injuries, patients could not remember what had happened to them for a period of time prior to the injury. The duration of such retrograde amnesia varied as a function of the severity of the injury. This suggested that the process of registering an experience in memory took some time and that the injured brain could not carry out this process. The process was labeled "consolidation."

During the 1960s and 1970s, James McGaugh and his collaborators (McGaugh & Hertz, 1972) carried out a series of experiments during which they interfered with, or enhanced, consolidation by injecting rats with different chemical substances immediately after they had experienced shock. The times of injection were varied in order to chart the course of the consolidation process. Once McGaugh had accomplished this he set out to locate the brain systems involved in the process. The amygdala seemed a good choice as a starting point in the search. Consolidation was now successfully manipulated by electrical and chemical stimulations much

as had previously been done by peripheral chemical injections. In any such series of experiments, however, the possibility remains that all one is accomplishing by the brain stimulation is the boosting of a peripheral chemical secretion so that in essence one is doing no more than repeating the original experiments in which peripheral stimulation had been used. To control for this, Martinez, working with McGaugh, removed various peripheral structures such as the adrenal gland. They found that indeed, when the adrenal medulla which secretes epinephrine and norepinephrine was absent, the amygdala stimulations had no effect (Martinez, Rigter, Jensen, Messing, & Vasquez, 1981).

McGaugh's experiments indicate, as had ours, that the amygdala influences the learning process via visceral and glandular peripheral processes which are largely regulated by the autonomic nervous system. Electrical excitation of the amygdala -- as well as of the entire anterior portion of the limbic cortex: anterior cingulate, medial and orbital frontal, anterior insula, and temporal pole -- in anesthetized monkeys and humans produces profound changes in such visceroautonomic processes as blood pressure and respiratory rate (Kaada, Pribram, & Epstein, 1949). The amygdala thus serves as a focus for a mediobasal motor cortex which regulates visceroautonomic and other activities (such as head-turning which is also produced by the stimulations) related to orienting. It appears from all this research that such peripheral activities when they occur, can boost the consolidation process and thus facilitate the registration of experience in memory. Vinogradova (1975) has suggested that the boost given by this visceroautonomic system stands in lieu of repetition of the experience. As noted above, the experiments on conditioning suggest that visceroautonomic arousal acts somewhat like internal rehearsal. One can take visceroautonomic arousal as an indication that interest and emotions have been engaged: thus the mechanism has been tapped which accounts for the well-known fact that emotional involvement can dramatically influence learning.

C. PROCESSING THE FAMILIAR

Context is not composed solely of the registration of reinforcing and reinforced events. As important are the errors, the non-reinforced aspects of a situation, especially if on previous occasions they had been reinforced. It is resection of the primate hippocampal formation (Douglas & Pribram, 1966) which produces relative insensitivity to errors, frustrative non-reward (Gray, 1975; and see Chapter 33, this volume, by Gray) and more generally to the familiar, non-reinforced aspects of the environment (the SΔ of operant conditioning: the negative instances of mathematical psychology). In their first experience with a discrimination learning situation subjects with hippocampal resections show a peculiar retardation provided there are many nonrewarded alternatives in that situation: For example, in an experiment using the computer-controlled automated testing apparatus (DADTA), the subject faced 16 panels; discriminable cues are displayed on only two of these panels and only one cue is rewarded. The cues are displayed in various locations in a random fashion from trial to trial. Hippocampectomized monkeys were found to press the unlit and

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

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

D. THE SPATIOTEMPORAL STRUCTURE OF CONTEXT

In some respects the far frontal resection produces memory disturbances characteristic of both hippocampectomy and amygdalectomy, though not so severe. Whereas medial temporal lobe ablations impair context formation by way of habituation of novel and familiar events, far frontal lesions wreak havoc on yet another contextual dimension, that of organizing the spatial and temporal structure of the context (Pribram, 1961; Anderson, Hunt, Vander Stoep, & Pribram, 1976; Pribram, Plotkin, Anderson, & Leong, 1977). This effect is best demonstrated by an experiment in which the normal scallop produced by a fixed interval schedule of reinforcement fails to develop and another in which the parameters of the classical alternation were altered. Instead of interposing equal intervals between trials (go right, go left every 5 seconds) in the usual way, couplets of R/L were formed by extending the intertrial interval to 15" before each R trial (R 5" L 15" R 5" L 15" R 5" L 15"...). When this was done, the performance of the far frontally lesioned monkeys improved immediately and was indistinguishable from that of the controls (Pribram & Tubbs, 1967; Pribram, Plotkin, Anderson, & Leong, 1977). This result suggests that for the subject with a bilateral far frontal ablation, the alternation task is experienced similarly to reading this page without any spaces between the words. The spaces, like the holes in doughnuts, provide the contextual structure, the parcellation or parsing of events by which the outside world can be coded and deciphered.

E. CONTEXT AS A FUNCTION OF REINFORCING CONTINGENCIES

Classically, disturbance of "working" short-term memory has been ascribed to lesions of the frontal pole. Anterior and medial resections of the far frontal cortex were the first to be shown to produce impairment on delayed response and delayed alternation problems. In other tests of context-formation and fitting, frontal lesions also take their toll. Here also impairment of conditioned avoidance behavior and of classical conditioning and of the orienting GSR is found. Furthermore, error sensitivity is reduced in an operant conditioning situation. After several years of

training on mixed and multiple schedules, the monkeys were extinguished over 4 hours. The frontally lesioned monkeys failed to extinguish in the 4-hour period, whereas the control monkeys did (Pribram, 1961).
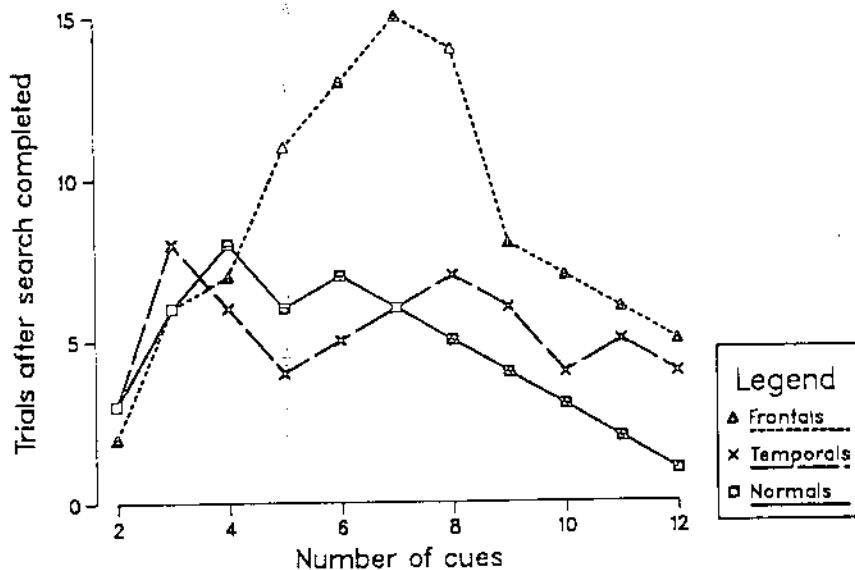

FIG. 34.9. The average number of trials to criterion taken in the multiple object experiment by each group in each of the situations after search was completed; that is, after the first correct response. Note the difference between the curves for the controls and for the frontally operated group, a difference that is significant.

This failure in extinction accounts in part for poor performance in the alternation already described: the frontally-lesioned animals again make many more repetitive errors. Even though they do not find a peanut, they go right back and keep looking (Pribram, 1959).

This result was confirmed and amplified in studies by Wilson (1962) and by Pribram, Plotkin, Anderson, & Leong (1977) in which we asked whether errors followed alternation or non-reinforcement. We devised a situation in which both lids over two foods wells opened simultaneously, but the monkey could obtain the peanut only if he had opened the baited well. Thus, the monkey was given "complete" information on every trial and the usual correction technique could be circumvented. There were four procedural variations: correction-contingent, correction-noncontingent, noncorrection-contingent, and noncorrection-noncontingent. The contingency referred to whether the position of the peanut was altered on the basis of the monkey's responses (correct or incorrect) or whether its position was changed independently of the monkey's behavior. We then analyzed the relationship between each error and the trial that preceded that error. Table 34.1 shows that for the

normal monkey, the condition of reinforcement and non-reinforcement of the previous trial makes a difference. For the frontally-lesioned monkey this is not the case. Change in location, however, affects both normal and frontal subjects about equally. In this situation, as well as in an automated computer-controlled version of the alternatives problem, frontal subjects are simply uninfluenced by rewarding or nonrewarding consequences of their behavior.

TABLE 34.2
Percentage of Alternation as a Function of
Response and Outcome of Preceding Trial

		Preceding Trial		
S	A-R	A-NR	NA-R	NA-NR
Normal				
394	53	56	40	45
396	54	53	36	49
398	49	69	27	48
384	61	83	33	72
Total	55	68	34	52
Frontal				
381	49	51	41	43
437	42	46	27	26
361	49	48	36	35
433	43	39	31	32
Total	46	46	33	33

Note-- S = Subject; A-R = Alternation and Reinforcement; A-NR = Alternation and No Reinforcement; NA-R = No Alternation and Reinforcement; NA-NR = No Alternation and No Reinforcement.

In the original multiple choice task (Pribram, 1959) (see Figure 34.9) the procedure called for a strategy of returning to the same object for five consecutive times, that is, to criterion, and then a shift to a novel item. The frontally-lesioned animals are markedly deficient in doing this. Again, the conditions of reinforcement are relatively ineffective in shaping behavior in animals with frontal lesions and the monkeys' behavior becomes nearly random when compared to that of normal subjects (Pribram, Ahumada, Hartog, & Roos, 1964). Behavior of the frontally-lesioned monkeys thus appears to be minimally controlled by the expected outcome.

F. TRANSFER LEARNING

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

A variety of other problem situations have demonstrated this relationship between the hippocampus and the previously non-reinforced (non-salient) aspects of a situation and between the amygdala and prior reinforcement. Multiple choice (Douglas, Barrett, Pribram, & Cerny, 1969) and distraction (Douglas & Pribram, 1966) experiments have been especially illuminating. In all instances, as in the reversal situations, whenever the probability structure of reinforcement becomes insufficiently distinct, or the distractions sufficiently powerful, limbic-lesioned subjects fail to persist in a strategy that had proved useful in prior situations. Attention and search are no longer directed (programmed) by previous experience; hypotheses are no longer pursued (Pribram, Douglas, & Pribram, 1969). The monkeys no longer expend the effort to maintain useful strategies and relapse to position habits which assure them a constant, if not a maximum number of reinforcements. In short, the monkeys become biased to caution. By contrast, resections of the inferotemporal cortex bias monkeys to risk (Pribram, Spevack, Blower, & McGuinness, 1980).

VI. CONCLUSION: LINGUISTIC LEARNING

The evidence presented here makes it not unlikely that one function of the posterior intrinsic and frontolimbic formations of the forebrain is to code events occurring within the input systems. As noted, the distribution of information (dis-membering) implies an encoding process that can reduplicate events. Regrouping the distributed events (re-membering) also implies some sort of coding operation – one similar to that used in decoding binary switch settings into an octal format and that into assembly and still higher-order programming language. An impaired coding process would be expected to produce grave memory disturbances. Lesion-produced amnesias, reference and contextual, therefore reflect primary

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Concretely, the intrinsic cortex is thus conceived to program, or to structure, an input channel. This is tantamount to saying that the input in the projection systems is coded by the operation of the intrinsic cortex. In its fundamental aspects, computer programming is a coding operation. The change from direct machine operation through assembler to one of the more manipulable computer languages involves a progression from the setting of binary switches to conceptualizing combinations of such switch settings in "octal" code and then assembling the numerical octals into alphabetized words and phrases and, finally, parcelling and parsing of phrases into sentences, routines, and subroutines. In essence, these progressive coding operations minimize interference among the configurations of occurrence and recurrence of the events.

This, then, is a sketch of the model derived from analyzing the effects on cognitive learning processes which resections and stimulations of the non-human primate brain have produced. What then distinguishes man's brain, identifies him as human? The psychopathology of human learning processes has almost universally been interpreted in terms of transcortical connections. All we have learned from experiments on non-human primate brains (e.g., the data described above) is evidence against the importance of such connections. Either the interpretation of the basis for the learning deficiencies in man is in error or else we have, through our efforts, stumbled on the difference between man's brain and that of his primate relatives. Thus it becomes paramount to review and test out once again, from this new vantage, the clinical evidence.

The converse of this approach has also proved fruitful. Experiments have tested the linguistic abilities, one-by-one, of non-human primates. The results have shown marked differences in syntactic competence which depends for its development on procedures which determine perceptual, motor and referential skills. In turn, such development depends on the construction of contexts from episodes and flexibly shifting these contexts in accordance with the spatiotemporal probabilities of reinforcement. These results indicate that the difference between non-human and human primates encompass a great deal of their forebrain and that these differences may well be due to an increase in transcortical connectivity.

ACKNOWLEDGMENTS

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