

## Chapter 14

# THE PRIMATE FRONTAL CORTEX – EXECUTIVE OF THE BRAIN

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### I. INTRODUCTION

The gross anatomical conglomerate anterior to the central fissure is given, in primate brains, a certain distinctiveness by the development of a bony orbit and is thus labeled the frontal lobe. Its posterolateral extent receives projections from the ventral thalamic nucleus and is covered with an agranular or dysgranular cortex. It constitutes the classical precentral motor cortex from which movements can be elicited at low thresholds by electrical excitation.

The remainder of the lobe, the subject of this essay, although somewhat homogeneous in its phylogenetic derivation and in its function, is made up of functionally discrete parts. A large portion of its medial extent derives projections from the anterior thalamic nuclei (Pribram and Fulton, 1954). Within this region, three subregions can be discerned, a supracallosal, a precallosal, and a subcallosal, each receiving projections from one of the anterior group of thalamic nuclei. Near the callosum the cortex covering this medial frontal region is transitional, junctional in type, and dysgranular; in keeping with these characteristics, it is found to give rise to movements when electrically stimulated (Kaada *et al.*, 1949) and so (with the orbitoinsulotemporal cortex, see next paragraph) has been labeled a mediobasal motor cortex (Pribram, 1961a). The precallosal portion of the region, further forward, is homotypical and eugranular in architecture, as is most of the remainder of the frontal lobe. This remainder, comprising the polar and lateral reaches of the lobe, receives projections from the major microcellular portion of the medial thalamic nucleus. The function of this cortex is the substance of this chapter.

Before proceeding to this discussion, however, we shall note another area of dysgranular transitional cortex important to the picture of the frontal cortex as a whole. This area lies on the posterior portion of the orbital surface, sandwiched between the orbital extensions of the medial and lateral cortices. This posterior orbital cortex derives its projections (Pribram *et al.*, 1953) from the midline of the thalamus (the midline magnocellular portion of the nucleus medialis dorsalis) and is heavily and reciprocally connected with the adjacent anterior insular, periamygdaloid, and temporal polar cortex (Fulton *et al.*, 1949).

In summary, apart from the classical precentral motor cortex, the primate frontal lobe can be divided into three major parts: (1) the medial, defined by its projections from the anterior nuclear group; (2) the dorsolateral (including the pole), defined by its projections from the microcellular portion of the medial thalamic nucleus; and (3) the posterior orbital, deriving projections from the midline of the thalamus and so heavily connected to the adjacent anterior insula, temporal pole and periamygdaloid cortex that these structures have often been considered together as a unit (Pribram and Bagshaw, 1953).

These anatomical considerations are important because investigators using behavioral techniques for the analysis of brain function have often ignored them, with consequent confusion in experimental results and their interpretations. Of special importance here are recent experiments in which large dorsolateral frontal resections have been compared with resections of the orbital cortex (Mishkin, 1964; Stamm and Rosen, 1973; Mahut, 1964; Pinsker, 1966). As noted, the orbital surface includes three different divisions: medial, lateral, and posterior. Differences in results obtained in various investigations might well be expected when different amounts of cortex from each of these categories have been included in the lesion.

Nonetheless, attempts to treat the frontal tissue selectively have proved to be most worthwhile. In order to ascertain for myself what the reported results might mean when comparison was made between lesions anatomically appropriate to each of the major divisions (excluding the precentral motor cortex), I prepared separate groups of monkeys with medial frontal, dorsolateral frontal, and orbitoinsulotemporal resections. With respect to alternation behavior (see Section V), at least, the effect of the dorsolateral lesion could be distinguished from that of the other lesions (Pribram *et al.*, 1966a; Figure 1). This finding reinforced my view that the effect on behavior reported by other investigators resulted from invasion into medial and orbitoinsulotemporal portions of the frontal lobe—portions which have in recent years been included under the rubric "limbic systems" because of their position at the inner edge of the cerebral hemisphere, their allo- or juxtallocortical cytoarchitectonics, and their functional relatedness (Pribram, 1958, 1961a).

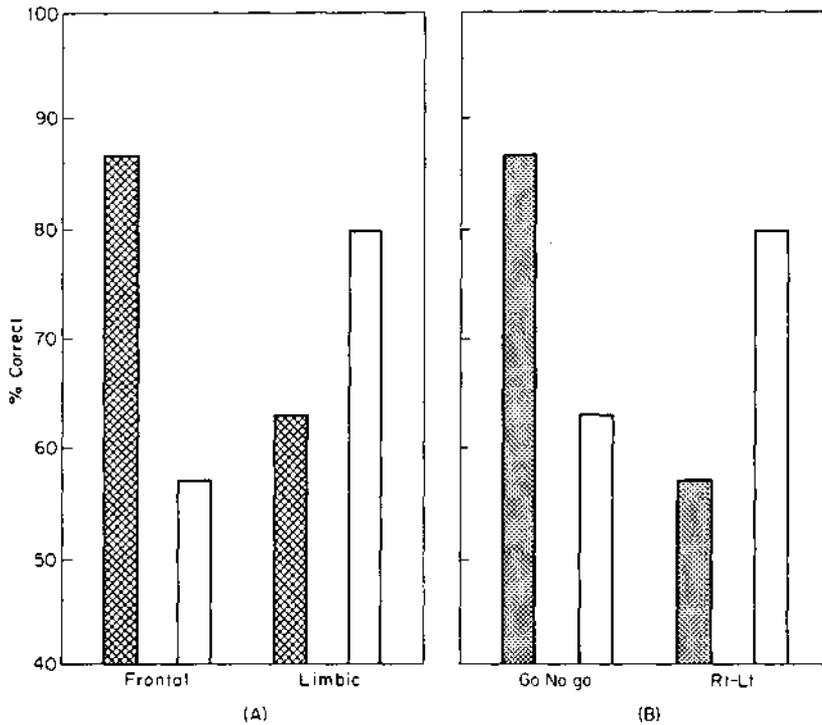


FIG. 1. Comparison of the effect of frontal and limbic lesions on (A) go-no go (cross-hatched bars) and right-left alternations (open bars). Comparison on the basis of lesion locus. (B) Comparison on the basis of task. Stippled bars represent the frontal group, open ones the limbic group.

## II. SPATIAL AND TEMPORAL ORGANIZATION

Despite this clarification, another, perhaps more serious problem of interpretation was aggravated by the results of the alternation experiments (Mishkin and Pribram, 1955, 1956; Pribram *et al.*, 1966b). Alternation behavior is disrupted by lesions anywhere in the frontolimbic formations (and also in some parts of the basal ganglia) but not by lesions in the sensory-motor projection systems or in the cortex associated with these systems. Its temporal organization is the characteristic of the alternation task. This leads to an hypothesis that the frontolimbic formations might be directly involved in providing the temporal structure necessary to the proper execution of all behavior.

The hypothesis was put to test and found to be only partially supported. The sequential organization of behavior (pressing without repetition a series of

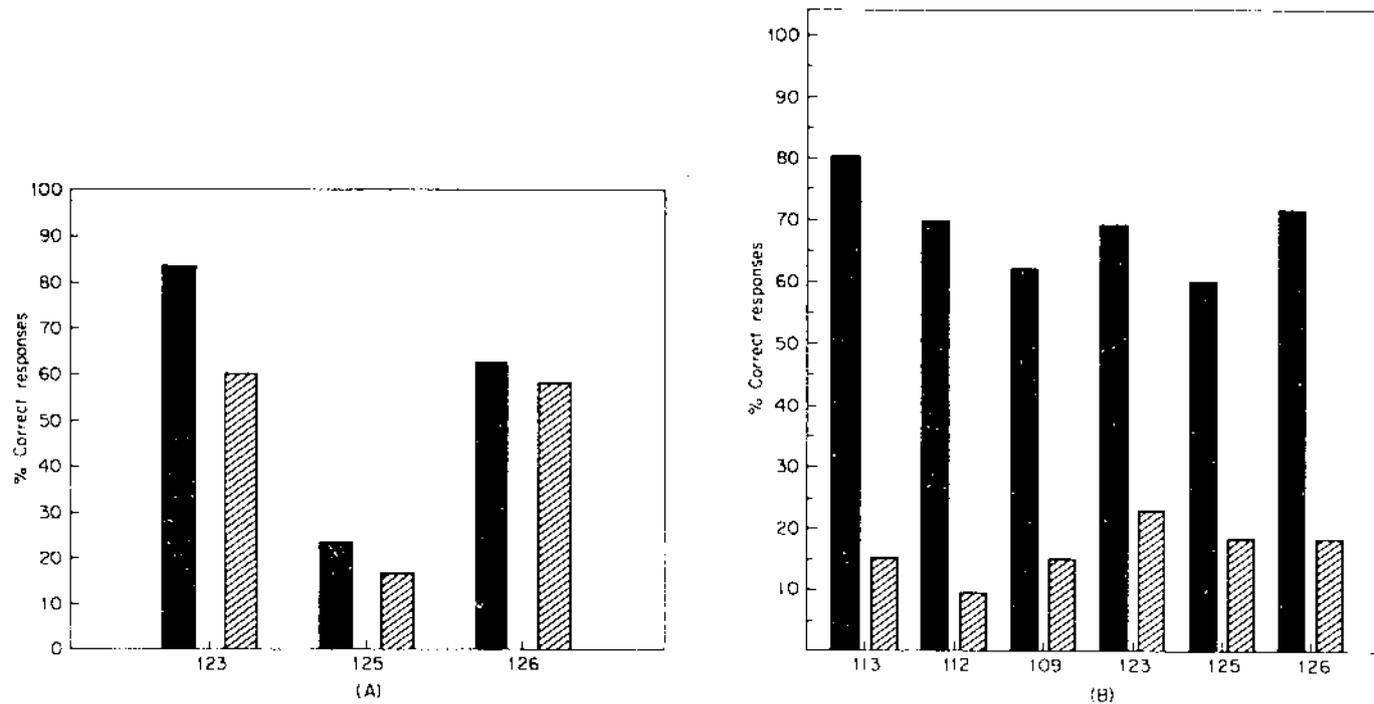


FIG. 2. (A) Percentage of correct responses in the pre- (solid) and postoperative (hatched) retention test for three monkeys with frontal lesions on the externally ordered sequence G-R. (B) Percentage of correct responses in the pre- (solid) and postoperative (hatched) retention test for frontal and temporal groups on the internally ordered sequence G-O-'4.'

spatially randomized panels displaying distinct symbols) is indeed disrupted by frontal lesions, but only if that organization must be supplied by the monkey. (Figure 4). When external cues to organization are supplied by the procedure (as when reinforcement is contingent on pressing, on each trial, the identical order of symbols), frontally lesioned monkeys perform as do their unoperated controls (Pinto-Hamuy and Linck, 1965; Figure 2).

Another serious doubt about interpreting the frontal syndrome in purely temporal terms was raised by the finding that frontal lesions produce greater disturbance in spatial than in nonspatial and go-no go problems (Pribram and Mishkin, 1956; Pribram *et al.*, 1952). This led to the inference that the dorso-lateral frontal cortex is somehow essential to the processing of spatial cues (Mishkin, 1964; Figure 3).

That this simple interpretation must be modified has been shown by a subsequent study (Pohl, 1970). In this experiment, two different spatial tasks were devised: one to test for responses based on external, the other on internal spatial cues. In the external cue task, the monkey had to respond to the location nearest a signal object, which varied from side to side. In the other (Figure 4), the monkey had to respond repetitiously to one side. Once these criteria had been attained, the problem was reversed: now reward went to responses away

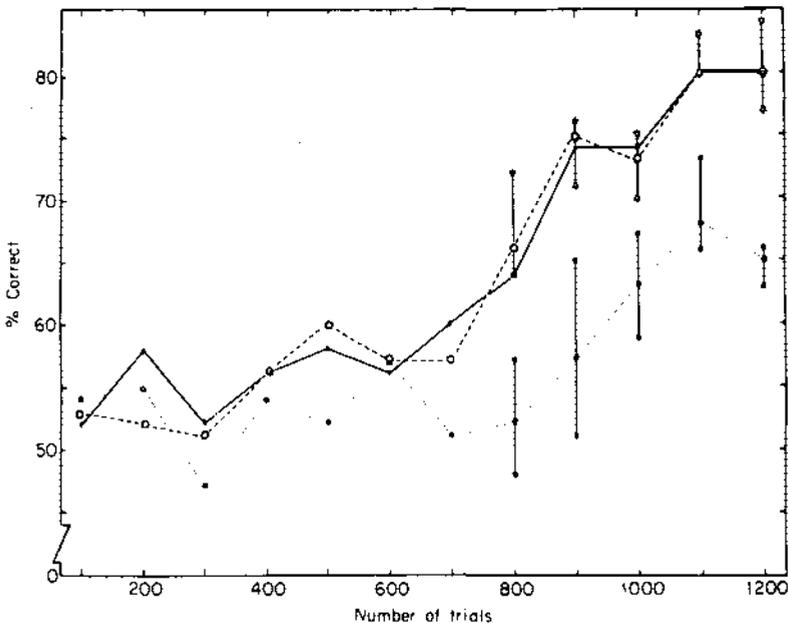


FIG. 3. Performance graph for monkeys in the nonspatial object alternation experiment. (\*) Normals; (o) temporals; (◐) frontals. Vertical lines show range of data.

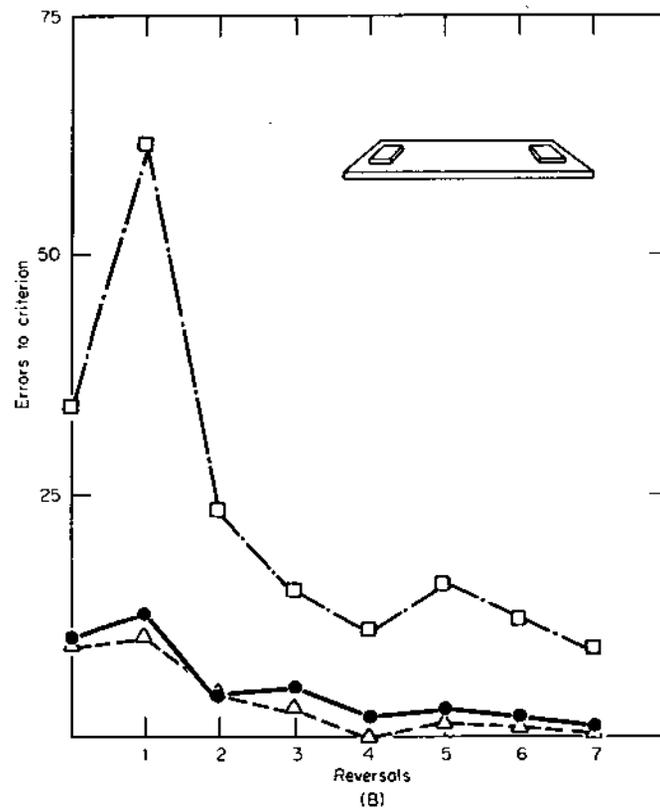
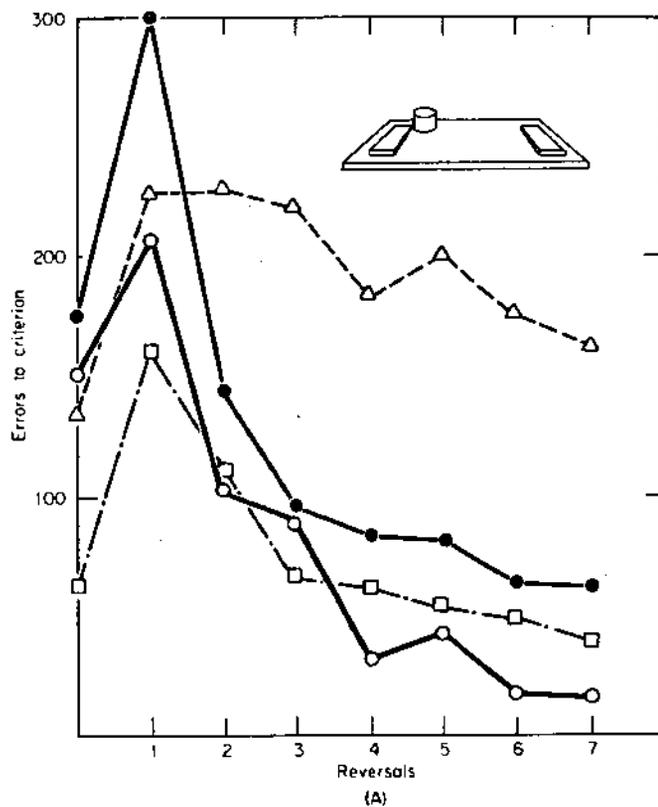


FIG. 4 (A) Performance of unoperated controls and three lesion groups on the landmark reversal task. (●) Temporal; (Δ) parietal; (□) frontal; (○) unoperated. (B) Performance of lesion groups on the place reversal task. Symbols as in Fig. 3A.

from the signal and, in the second test, to responses made to the side other than before. Monkeys with parietal lobe lesions failed the externally (but not the internally) cued task, whereas the frontally lesioned monkeys were severely hampered in their internally (but not the externally) cued performance.

### III. DISTRACTION: PROACTIVE AND RETROACTIVE INHIBITION

Thus, both the temporal and spatial organization of behavior are disrupted by frontal lesions when, and only when, that organization is incompletely specified by environmental contingencies. In such situations, the organization of behavior becomes dependent upon internal processes. What might these processes be and by what mechanisms are they effected?

A clue to the answers to these questions comes from the results of the following experiment (Grueninger and Pribram, 1969). Monkeys were trained to respond quickly in succession to two cues. Then another cue, a distractor, was introduced simultaneously with the second cue and the consequent change in latency of response to the succession of cues was recorded. Two types of distractors were used, spatial and nonspatial. Monkeys with dorsolateral frontal resections were distracted more than unoperated controls by spatial interpolations and, moreover, they reacted more to spatial than to nonspatial distractors. Thus, an explanation for the observation that frontal lesions affect spatial delay problems more than nonspatial, can be suggested: dorsolateral frontal lesions do not preclude the processing of spatial information; instead, such lesions make the organism more sensitive to distraction, especially by spatial cues, a condition not unlike that found in unoperated but naive monkeys (Figure 5).

This result makes plausible the hypothesis that shifts in the spatial dimension in the spatial alternation problem act as distractors, interfering with adequate performance on the task, whereas shifts in the nonspatial dimensions are less distracting. The greater difficulty experienced by frontally lesioned monkeys on spatial tasks would thus be accounted for.

In earlier experiments (Malmo, 1942), monkeys were run under a variety of conditions designed to minimize interference. An explanation in terms of retroactive and proactive inhibition was set forth and became the classical way to account for the impaired performance of frontally lesioned animals on the spatial delayed response problems, the other task typically failed by such animals. The interference hypothesis is at present, as it has been for three decades, the most viable and useful in explaining the effects of resection of the dorsolateral frontal cortex of primates. This would suggest the hypothesis that under ordinary conditions the frontal cortex functions to inhibit interference.

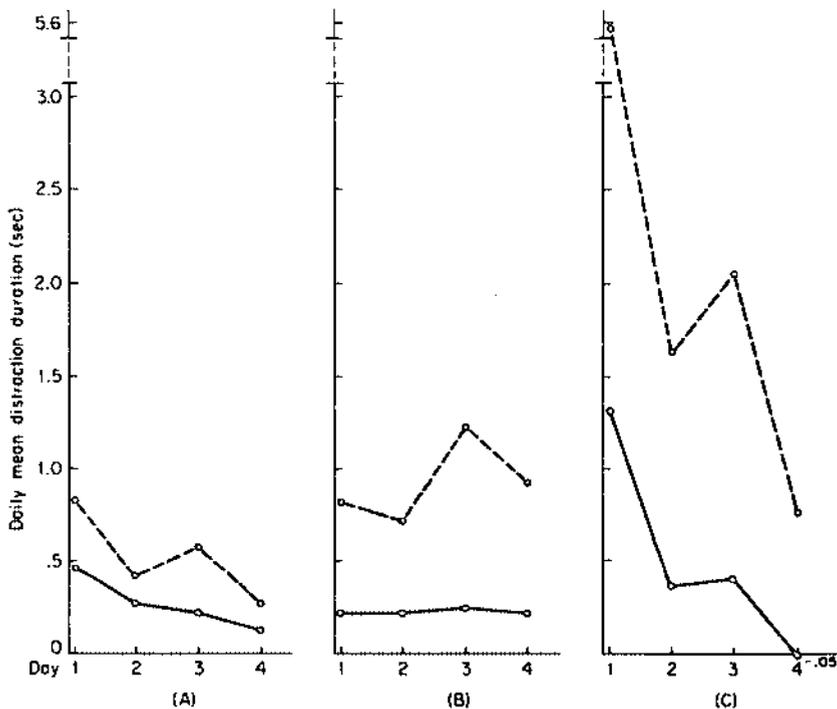


FIG. 5. Daily mean distraction duration (mean distraction trial latency minus median latency) for (A) condition 1: stimulus varied, location constant; (B) condition 2: location varied, stimulus constant; and (C) condition 3: buzzer. (○) Frontals; (○) normals.

The remainder of this chapter will be devoted to detailing the results of experiments aimed at obtaining an understanding of the mechanisms of inhibition of interference by the frontal cortex. A synthesis will be attempted in terms of a model. Perforce, this chapter will concentrate on the functions of the dorso-lateral frontal cortex, leaving those of the limbic (medial and orbitoinsulo-temporal) formations for another occasion. However, from what has already been reviewed, it should be clear that the point of view entertained here is that all three of the anterior frontal regions are concerned in this function.

#### IV. CONTROL OF INPUT

Two methods for investigating the mechanisms of frontal influence on the inhibitory organization of brain processes were explored. One consisted of continuing the studies of the effects of frontal resection on behavior; the other

employed psychophysiological and neurophysiological techniques to record the effects of frontal resections on the processing of input to the brain. The experiments on input control stemmed from a series of studies using the delayed response and alternation tasks that showed that reaction to cue variables rather than response contingencies were affected by frontal resection (Mishkin and Pribram, 1955, 1956; Pribram and Mishkin, 1956). In these studies, the procedure was changed from a go right-go left situation to a go-no go task. This change resulted in a surprising improvement in the performance of the delay tasks by frontally lesioned monkeys, which could be attributed either to the change in response choice or to the change in cue (bait versus bare hand in delayed response; having just responded or withheld a response in the alternation task). Further experimentation showed that, in fact, it was the change in the cues, not in the response choice, that made the difference. When, in the delayed response task the original two-cup situation was retained and the monkeys cued to the left cup by a peanut and to the right cup by a bare hand displayed between the two cups, the monkeys performed as well as in the go-no go procedure. Also, when responses had to be alternated between two objects, irrespective of their placement, alternation performance improved. The results of these experiments supported the interference hypothesis and so will be taken up first. [It should be noted that these data also gave rise to the spatial hypothesis as an explanation for the effects of frontal damage, an hypothesis that continued to be supported by other results until found partially wanting by the results of Pohl's (1970) experiments, described earlier.]

Because in an earlier experiment monkeys with frontal lesions were found to react behaviorally with alacrity to novelty even under conditions when control subjects did not (Pribram, 1960), an investigation of the effect of such lesions on the orienting reaction seemed in order. Sokolov (1960) had just described the physiological measures of orienting in detail; of these, the galvanic skin response (GSR) was the simplest to use and so was applied to the study in frontal patients (Luria and Homskaya, 1964; Luria *et al.*, 1964) and monkeys (Kimble *et al.*, 1965). Much to our surprise, this and other psychophysiological measures failed to confirm the behavioral observations of distractibility, i.e., hyperreactivity to novelty; just the opposite was found. Psychophysiological measures of orienting did not occur at all (Kimble *et al.*, 1965), or if they did, they were sluggish in their appearance and disappearance (Grueninger *et al.*, 1965). Could it be that the absence of the psychophysiological components of orienting is directly related to the hyperreactivity to novelty and continued distractibility? Are these psychophysiological reactions perhaps indicative of a mechanism necessary for behavioral habituation to take place?

Further analysis suggested that this was indeed the case. The orienting reactions described by Sokolov (1960) could be classified into at least two categories: those involved in sampling the situation and those necessary to register it in awareness and memory. Registration appears to be necessary for

behavioral habituation to occur (Kimble *et al.*, 1965; Bagshaw and Benzies, 1968). Frontal lesions, by interfering with registration, make the organism susceptible to changes in input to which normal subjects had become accustomed, i.e., habituated (Figure 6).

Next, it became imperative to check whether one could obtain any direct neurophysiological evidence for frontal control over input processing. This evidence was obtained in the following manner (Spinelli and Pribram, 1967). Small gross electrodes were implanted in the visual system and records were made in the fully awake monkey faced with paired bright flashes of light. Computer summation (averaging) techniques were used to enhance the reliably repetitive aspects of the neuroelectric responses evoked by the flashes. The amplitude of the pair of responses was measured and that of the second response expressed as a percent amplitude of the first. During the experiment, the

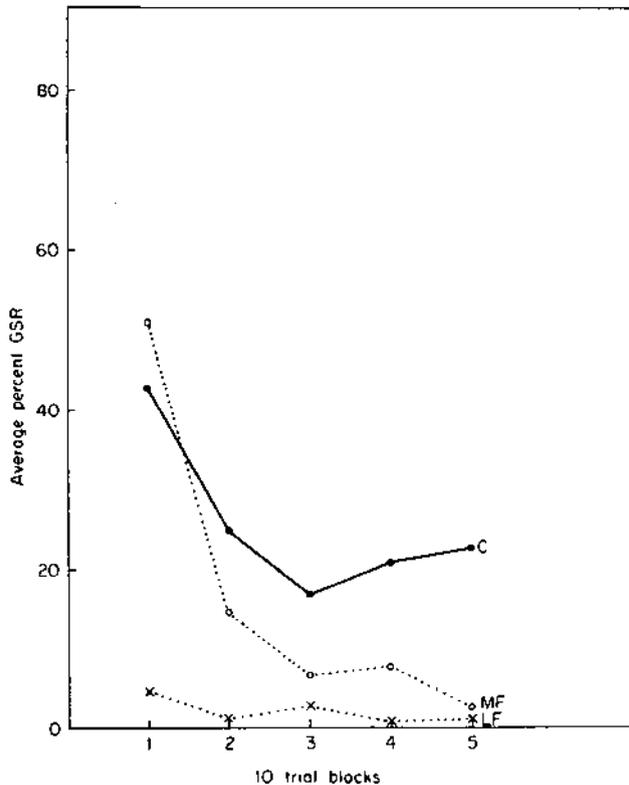


FIG. 6. Curves for percent GSR response to the first 50 presentations of the original stimulus on the second run for the normal (CH), medial frontal (MF), and lateral frontal (LF) groups.

interflash interval separating each pair of flashes was systematically varied and the percent amplitude was plotted as a function of the interflash interval. This provided a recovery function that indicated the percent of the visual channel available for processing the second of the pair of flashes when it occurred.

A stable recovery function served as a base line for testing the possible effects of electrical stimulation of the frontal cortex. As shown in Figure 7, an effect was obtained, recovery was markedly enhanced by the frontal lobe excitation.

To test the validity of this result, microelectrodes were inserted into various levels of the visual channel and visual receptive fields were plotted. Now, the effect of electrical excitation of the frontal cortex on stable (for over an hour)

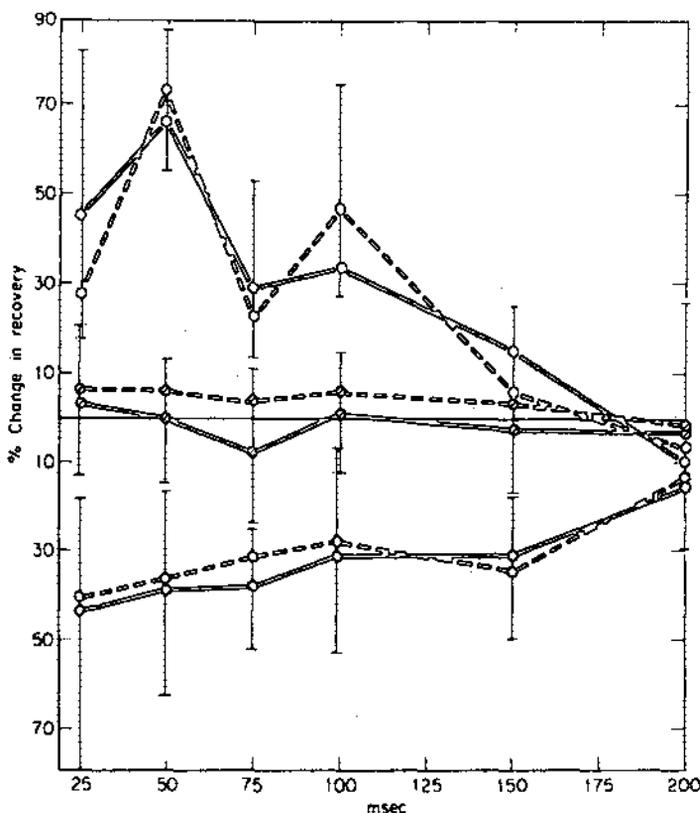


FIG. 7. The change in recovery of a response to the second of a pair of flashes compared with prestimulation recovery function. Control stimulations were performed on the parietal cortex. Records were made immediately after the onset of stimulation and weekly for several months. The response curves obtained immediately after onset (—) and after 1 month (---) are presented. Vertical bars represent variability of the records obtained in each group of four monkeys. (○) Temporal lobe stimulation; (◻) frontal lobe stimulation; (△) control stimulation.

receptive fields was explored and again a dramatic result was obtained (Figure 8). There can be no question that by an as yet unknown pathway the dorsolateral frontal cortex can exert an influence on visual input processing.

The simplest way to conceptualize this effect of the frontal cortex on the input channel in psychological terms is to suggest that it produces some alteration in the attentive process (Gerbrandt *et al.*, 1970). Unfortunately, the term *attention* is commonly used in a variety of ways. However, in frontal lobe function, some precision in its use has been provided by the results of the experiments that showed that registration was impaired in subjects with frontal lesions. The term *registration* thus implies a focusing of attention, an *assimilation*—to use Piaget's term—of the situation by the organism.

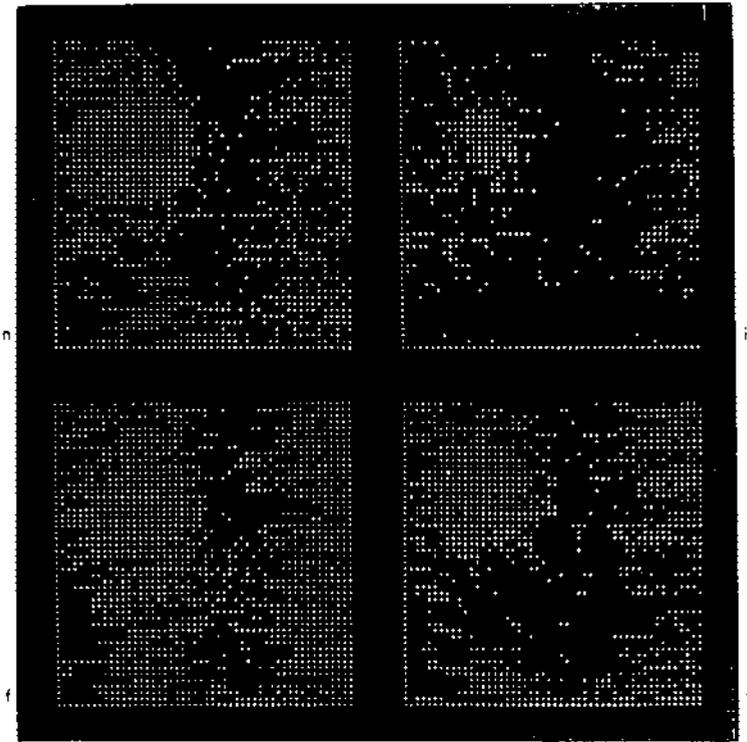


FIG. 8. Receptive field maps from a lateral geniculate unit. (n) Top left; control; (i) mapped while inferotemporal cortex was being stimulated; (f) mapped during frontal cortex stimulation; (n) bottom right, final control. A third control was taken between the (i) and the (f) maps and was not included because it was not significantly different from the first and the last. Note that inferotemporal stimulation (i) decreases the size of the "on" center; frontal cortex stimulation (f), although not really changing the circular part of the receptive field, brings out another region below it. The level of activity shown is three standard deviations above the normal background for this unit.

## V. THE FRONTAL CORTEX AND BEHAVIOR

To return now to the other major method for investigating inhibition of interference among the brain's processing mechanisms: the continuing experimental analysis of behavioral disturbance produced by frontal lesions. What might be the effects on behavior of a deficiency in registration, an impaired process of assimilation? William James noted that, "what holds attention determines action." And as already mentioned, frontally lesioned monkeys continue to react to cues as if they were novel long after control subjects have behaviorally habituated to them.

Interestingly and somewhat surprisingly, however, the deficiency appears even more dramatically in a different aspect of behavior determination: monkeys with frontal resections do not process the consequences of their behavior as do normal animals (Pribram, 1960). Reinforcement, whether reward, punishment (English and Rosvold, 1956; Pribram, 1961b), or error (Pribram, 1961b), is processed sluggishly by the operated subjects. In a sense, this deficit is most obviously apparent in classical conditioning situations, where even reinforcement by punishment is severely affected (Rosvold and Szwarcbart, 1964). This inability to stably maintain reward-guided behavior is manifest in the two-choice discrimination (Pribram *et al.*, 1966a), and becomes critical in a multiple-choice situation in which monkeys are expected to reach a criterion of five consecutive errorless trials. In this task, frontally lesioned subjects will repeatedly make three and even four correct responses and then make an error, thus delaying the attainment of the criterion (Pribram, 1961b). In fact, the failure to perform the classical, spatial, delayed alternation task (Figure 9) has been shown by W. A. Wilson (1962) to depend for its solution on just this same insensitivity to reinforcing stimuli: frontally lesioned monkeys have difficulty in remembering the position of the preceding reinforcer. Moreover, even when the successive form of alternation is presented, a form which, as noted earlier, frontally lesioned monkeys can learn to perform, learning is characterized by an extraordinary number of errors (Pribram, 1960; Figure 10).

These results raise questions about the relationship of attention, at least in its registrational aspects, to reinforcement. Must reinforcers be registered in awareness or only in memory in order to guide behavior? Just what is the connection between awareness and memory? Does attention invariably imply awareness? Is one function of reinforcers to attract attention or is behavior guided by them without such an intervening step in most instances? The answers to these questions are not at present available but should be forthcoming as a result of experiments in which responses are observed in animals and man using the elegant techniques developed for eyeball photography accomplished while the subject is performing a task (Mackworth, 1967, 1968). When man is the subject, the relationship between attention and awareness should be subject to check by

asking for a verbal statement describing awareness and correlating this with the evidence from the eye camera and perhaps even with some concomitant neuroelectric measurements.

## VI. THE MODEL

I feel reasonably sure that the dorsolateral frontal cortex, like the limbic formations of the forebrain (including the medial and orbital frontal cortex), are concerned in the inhibition of interference among brain events. With respect to lesions of the frontal cortex, this involvement becomes manifest on the input side as a difficulty in attention, a difficulty in registering novelty so that habituation, or assimilation, fails to take place. On the output side, the feedback to actions from their outcomes is impaired and reinforcers become relatively ineffective.

The intact frontal brain tissue must help to accomplish registration and reinforcement by some not too complicated mechanism. What could be its nature? In order to obtain some clue, I turn, as I so often have in the past, to the analogy of those hardware brains, especially computers, that so effectively mimic many of the functions ordinarily carried on by the wetware in our heads (Miller *et al.*, 1960; Pribram *et al.*, 1964; Pribram, 1971). Mechanical as well as biological thinking machines continually face the simultaneous demands of a variety of inputs and outcomes. These could easily interfere with one another and with any of the central operations being carried on at the moment by the computer. To prevent this, some noticing order must govern the acceptance of first this, then that, product of the input-output devices. In its simplest form, each of these devices is fitted with a marker or flag, which decrees that while busy with its productions, the computer temporarily shuts off the paths to and from other

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FIG. 9. Graph showing the differences in the number of repetitive errors made by groups of monkeys in a go-no go type of delayed reaction experiment. Especially during the initial trials, frontally operated animals repeatedly return to the food well after exposure to the nonrewarded pre-delay cue. Note, however, this variation of the delay problem is mastered easily by the frontally operated group. The 12 rhesus monkeys used in the multiple object experiment had served as subjects some 2 years earlier in the delayed response experiment portrayed here. (—) Normals; (---) temporals; (···) frontals.

FIG. 10. Graph of the average number of trials to criterion attainment taken in the multiple object experiment by each of the groups in each of the situations after search was completed, i.e., after the first correct response. Note the difference between the curves for the controls and for the frontally operated group, significant at the .05 level by analysis of variance ( $F = 8.19$  for 2 and 6 df) according to McNemar's (1955) procedure performed on normalized (by square root transformation) raw scores. (—) Normals; (---) temporals; (···) frontals.

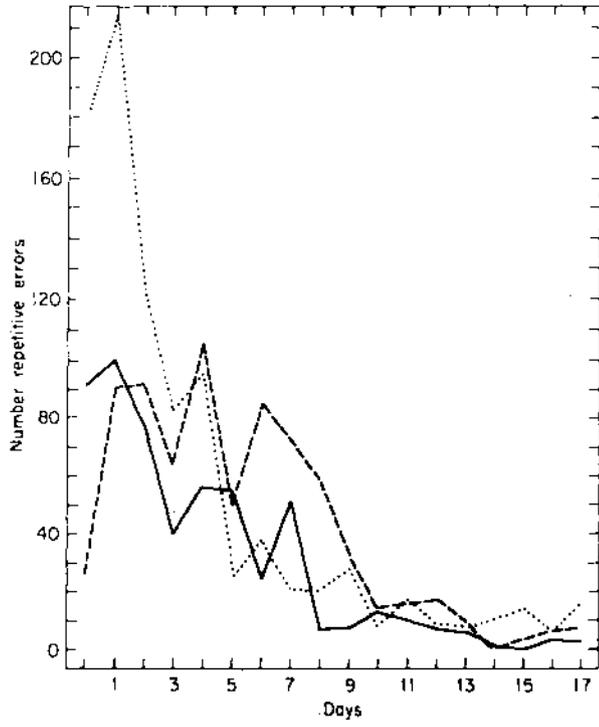


Figure 9

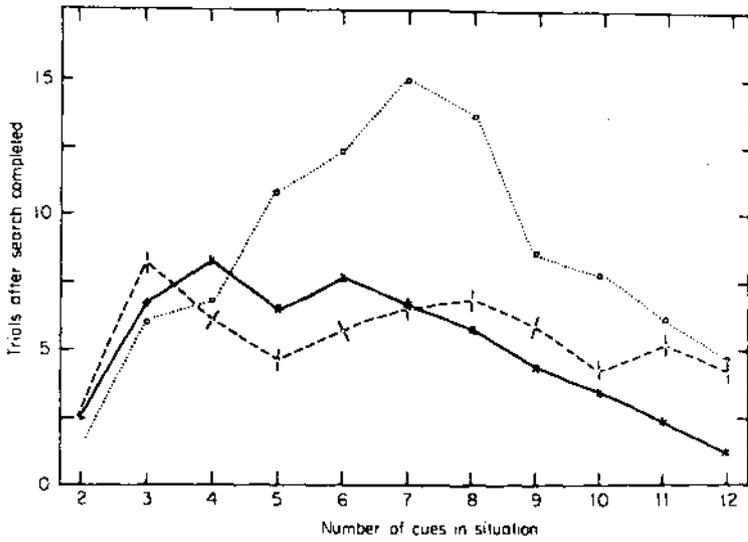


Figure 10

devices. In more complicated forms, only part of the computer may be thus preempted, or a program can be used to regulate the flow of information. Simple flexible noticing order programs have been used for years for this purpose; more recently these have burgeoned into full scale executive routines that effect the timesharing of large multiple user machines.

The essence of flexible noticing orders is their multiply recursive nature. Instead of the branching hierarchy that characterizes programs used to make discriminations and to compute, flexible noticing orders must in some way keep track of the various routines that involve the computer. Which routine has precedence depends upon an order that can be flexibly rearranged according to other flexible programs. What is allowed to occur at any moment, therefore, is weighted on the basis of a number of simultaneously noticed events. What occurs becomes dependent upon the context of these noticed events. The structure of programs with such characteristics is called *context sensitive* or *context dependent*, whereas the structure of hierarchical programs is said to be *context free*, because the occurrence of a particular item in the program is completely specified by the hierarchy of the routine in which it occurs. As already described, frontal lesions have their effect on behaviors that are incompletely specified by the environmental situation (schedules, routines) in which the behavior takes place. It is therefore plausible to hypothesize that the frontal cortex is especially concerned in structuring context-dependent behaviors.

To put this in slightly different terms, in a simple sensory discrimination (whether a simultaneous or a successive procedure is used), the cue-response-reinforcement contingencies remain invariant across trials. The close coupling of appropriate behavior to this invariance makes it free of determinants at other levels. In the delayed response and alternation tasks, on the other hand, these contingencies vary from trial to trial and the subject must take note of these variations so that second-order invariances can be extracted. These second-order invariances provide a context in which appropriate behavior is generated. It is in this sense that the behavior becomes context dependent.

On an earlier occasion, I had already compared the functions of the frontal cortex to that of a flexible noticing order, a primitive executive program (Pribram *et al.*, 1964). I suggested then that Ukhtomski's (1926) "dominant focus" might provide the neurological mechanism by which flexibility in noticing order might be achieved. It remains here to bring this model up to date by alterations and specifications made possible by the neurophysiological and neurobehavioral results that have accrued since the proposal was made.

Two findings are of special significance. One concerns the recovery function data reported in this manuscript. The other was provided by the discovery by Grey Walter (1964) of a contingent negative electrical variation (CNV) originating in the front part of the brain whenever an organism is preparing to perform (i.e., during the foreperiod) in a reaction-time experiment. This rather

extensive neuroelectric phenomenon certainly behaves as a temporary dominant focus. Could it be a signal that the brain is busy and act as an interference prevention device blocking input, much as does the marker or flag in mechanical computer systems? Partial answers to this question might come from experiments that study the relationship between this electrical brain event and those that are involved in the registrational aspects of the orienting reaction, like the experiments by Lacey (1969) on the foreperiod (readiness to respond) phenomenon. As noted elsewhere in this volume (Chapter 7), such experiments have shown the frontal cortex to be especially active in the production of the CNV in tasks where behavior has not as yet become completely dependent upon environmental contingencies--when a marker or flag is especially necessary to prevent distracting interference (Donchin *et al.*, 1971).

The importance of the recovery function data for frontal lobe function is somewhat more complicated to present because a neuronal minimodel of the recovery cycle phenomenon must first be constructed. This minimodel has been detailed on several occasions (Pribram, 1968, 1971): in essence it is based on the inhibitory interactions that occur in the input channels. Two reciprocally related forms of inhibitory phenomena are recognized: those in which the activity of a neuron decreases that of its neighbors and those that result in diminishing the activity of the neuron itself. These two types of reciprocal afferent inhibition have been compared to Pavlov's *external* and *internal* forms, respectively. The suggestion was made that the usual function of the frontal cortex is to weight the balance of these reciprocal processes toward internal inhibition, i.e., self diminishing neural activity (Figure 11). This suggestion was based on the recovery function data, which showed that recovery of cells in the visual system excited by flashes was enhanced; i.e., cells returned to their preexcited state more rapidly.

The model was further developed (Pribram, 1971) to suggest that the orienting reaction and its habituation depended upon the activation of these reciprocal afferent inhibitory mechanisms: orienting on the contrast-enhancing effect of the inhibition of a neighbor's activity; habituation on the subsequent diminishing of this effect caused by the progressive diminution in the number of the initiating impulses.

## VII. TEST OF THE MODEL

The model is thus operationally spelled out at several levels. Neuronally, the effect of frontal excitation on afferent inhibitory mechanisms can be checked. At a somewhat grosser level, the effects of frontal excitation and resection on foreperiod and orienting responses can be investigated using eye movement

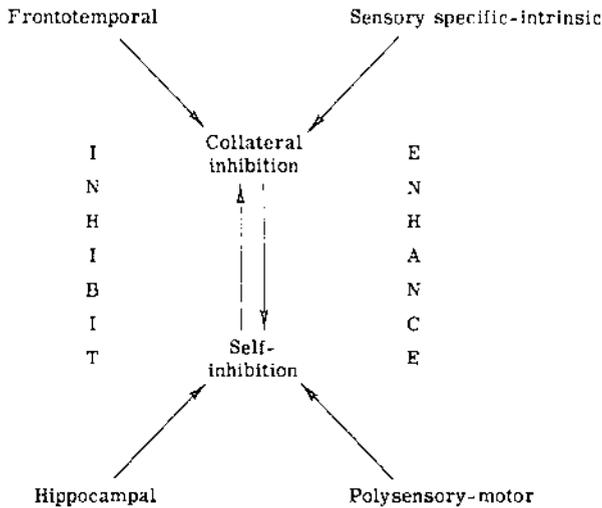


FIG. 11. A model of the inhibitory interactions taking place within the afferent channels. Collateral and recurrent afferent inhibitions are bucked against one another, forming a primary couplet of neural inhibition within afferent channels. Four forebrain mechanisms are assumed to provide efferent control on the primary couplet: Two of these, frontotemporal and sensory specific-intrinsic (which included the inferotemporal cortex), influence the couplet by regulating collateral inhibition; two others, hippocampal and polysensory-motor, regulate recurrent inhibition. The sensory specific-intrinsic and polysensory-motor association cortical systems exert their control by enhancing, whereas the frontotemporal and hippocampal systems exert control by inhibiting afferent neural inhibition.

recordings, the contingent negative variation, and other brain wave manifestations, as well as the more usual psychophysiological indicators (GSR, heart and respiratory rate changes, and alterations in blood flow). Finally, at the behavioral level, an attempt can be made to compensate for the deficiency produced by frontal lesions by providing the organism with a frontal prosthesis, as it were. Using such an external substitute for its frontal cortex, a lesioned monkey should be able to perform as well as an unoperated control in the delayed alternation situation. Perhaps by providing the operated monkey with context, a marker or flag, by building into the task a simple executive program, problems previously failed could in this fashion be solved.

Such an experiment was performed (Pribram and Tubbs, 1967). The usual equal interval that separates the alternation trials was modified by interposing a 15 sec interval between each R-L couplet (Figure 12). Thus if the classical 5 sec delayed alternation problem can be represented as R5-L5-R5-L5-5R-5L-5... , the variation here presented would read: R5L-15-R5L-15-R5L-15-R5L...

Monkeys who had failed to adequately perform the classical task after 1000 trials performed remarkably well on the variation within 250 trials, much as did

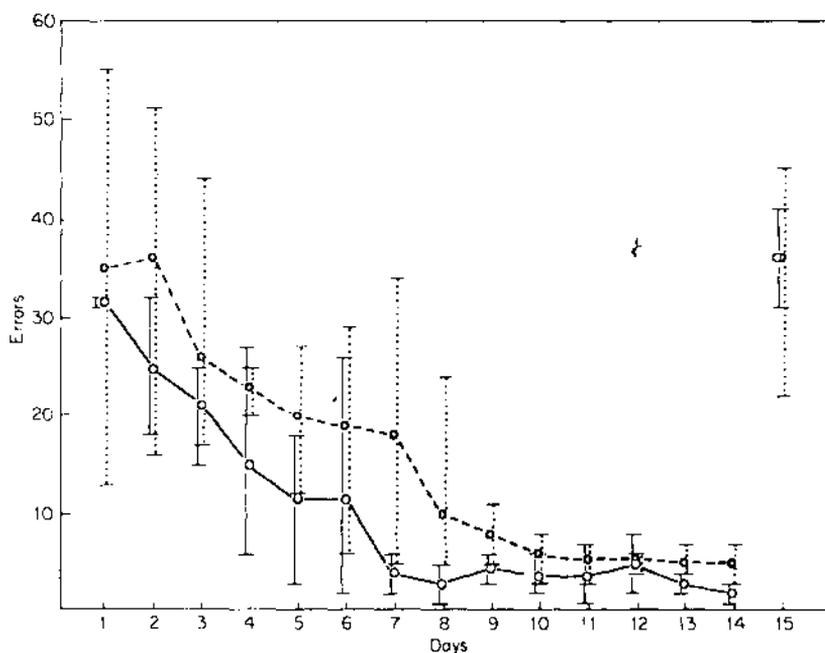


FIG. 12. Graph of the average number of errors made by monkeys having ablations of the frontal cortex ( $\odot$ ) and by their controls ( $\circ$ ). Bars indicate ranges of errors made. Records of the number of errors made on return to the classical 5 sec alternation task for day 15 are shown.

their normal controls. This dramatic improvement is not caused by changing the problem into a successive discrimination: interposing a red light or a loud buzzer as a marker for every other trial failed to produce such dramatic improvement in performance of either the control or the operated monkeys, although both control groups eventually (after 1000–1500 trials) learned to perform these tasks (Tubbs, 1969). Meanwhile, any return to the 15 sec interposition was immediately effective in restoring adequate performance in both operated and unoperated groups.

These results suggest that for the frontally lesioned primate, the alternation task and perhaps many other situations appear much as would this printed page were there no spaces between the words and no punctuation at the ends of phrases, sentences, and paragraphs.

Spaces serve as markers or flags to externally organize context-dependent input. The letters of the alphabet make meaningful organizations when arranged in different orders. This flexible order of arrangement is tolerated provided the length of the arrangement is limited (the magic number is  $7 \pm 2$ ; Miller, 1956).

The finding that, when context is furnished by markers, frontally lesioned primates can so readily perform a task that had been their nemesis for decades

supports the hypotheses that performance of this task is an instance of context-dependent behavior and that the function of the frontal cortex is, in the absence of sufficiently simple environmental structure, to internally organize a context upon which behavior must depend in such situations. In short, the frontal cortex appears critically involved in implementing executive programs when these are necessary to maintain brain organization in the face of insufficient redundancy in input processing and in the outcomes of behavior.

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