

THE PRIMATE FRONTAL CORTEX: PROGRESS REPORT 1975

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Studies of the functions of the cortex anterior to the motor regions of the brain have a venerable history. In non-human primates resections of this frontal eugranular cortex have been known for almost half a century to produce a very specific deficit in tasks characterized by the interposition of a delay between the occasion when a behavioral response is cued and when that response can be carried out. In man the procedure of frontal lobotomy or leukotomy and its various derivatives forms a chapter in the treatment of mental illness which has been variously evaluated as worthy of a Nobel prize and as morally degenerate. Further, the relationship between the results of the laboratory experiments on non-human primates and those obtained in the psychosurgical clinic has never become clear.

These deficiencies in our understanding of the functions of the primate polar frontal cortex are not due to neglect. Professor Konorski's efforts are well known and much appreciated by investigators the world over who have diligently pursued the problem. The results of their work can be found in two recent publications: *The Jabłonna Symposium on the Frontal Granular Cortex* edited by Konorski, Teuber and Żernicki (1972) and *The Psychophysiology of the Frontal Lobes*, edited by Luria and myself (1973).

Here, therefore, it is more fitting that an attempt be made to briefly review the highlights of the recent additions to this vast body of research; to report some as yet unpublished work which has bearing on our understanding of the frontal lobe problem; and to attempt to formulate a useful hypothesis about frontal lobe function based on these data.

The input-output relations of the frontal cortex

The major themes of the research of the past decade have been (a) to discover the critical input-output relationships between frontal (eugranular) cortex and the rest of the brain; (b) to subdivide the frontal (eugranular) cortex into functional subunits; and (c) to reach some better understanding of the functions affected by frontal resections and stimulations.

The input-output relationships between frontal eugranular cortex and other brain structures have been assessed by making resections or stimulations in most other brain locations to see whether such manipulations influence the performance of delay tasks. Manipulations of most brain structures do not affect such performances (Pribram 1954).

A major puzzle to investigators has been the fact that input to this cortex from subcortical structures derives almost exclusively from the nucleus medialis dorsalis of the thalamus, an intrinsic nucleus (i.e., one which derives its subcortical connections largely from other thalamic structures). Yet resections or stimulations of this thalamic nucleus do not, as a rule, disturb delay task performance (Chow 1954, Peters, Rosvold and Mirsky 1956). By contrast, when the limbic formations are invaded, e.g., amygdala, hippocampus and cingulate cortex, performance of some, though not all, delay tasks becomes markedly deficient (Pribram, Mishkin, Rosvold and Kaplan 1952, Pribram and Fulton 1954, Pribram, Wilson and Connors 1962). The only other brain structures consistently involved in influencing delay task performance are the head of the caudate nucleus and related parts of the globus pallidus and thalamus, the centrum medianum (see for instance early experiments by Rosvold: Rosvold and Delgado 1953; and by Pribram: Migler 1958; reviewed and extended by Rosvold and Szwarcbart 1964, and Rosvold 1972).

These results suggest that the frontal eugranular cortex has special functional affinities with the limbic forebrain and with parts of the basal ganglia. This suggestion is supported by the finding that the head of the caudate nucleus and the amygdala respond with extremely large electrical potential changes when the frontal eugranular cortex is stimulated (Pribram, unpublished results) and anatomical techniques have shown major connections to these structures (Whitlock and Nauta 1956, Kemp and Powell 1970).

Thus, the involvement of frontal cortex in delay tasks is not a function of input to that cortex but of the complex relationships among structures of the frontolimbic forebrain and especially between these and the output functions of the amygdala and the caudate nucleus of the basal ganglia.

Some functional subunits

Recent research has also emphasized the diversity of the functions of the frontal cortex anterior to the motor regions. Though generally related to delay tasks, the type of task influenced by limited resections differs depending on whether dorsal, ventral or orbital cortex is resected or stimulated (e.g., early experiments by Blum 1949, 1952; by Mishkin 1957; and by Pribram, Lim, Poppen and Bagshaw 1966; and more recent studies by Passingham 1974; and by Oscar-Berman 1975). In general,

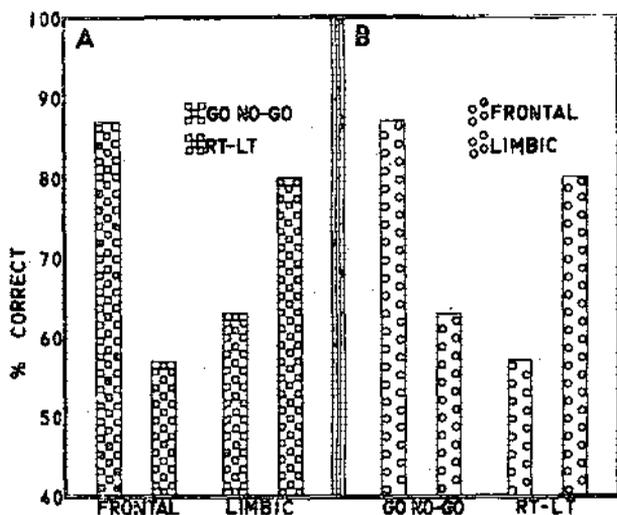


Fig. 1. Comparison of the effect of frontal and limbic lesions on (A) go-no go and right-left alternations. Comparison on the basis of lesion locus, B, comparison on the basis of task. Darkened circles represent the frontal group, open ones the limbic group.

these studies suggest that spatial delay tasks are affected by dorsal cortex manipulation; that visual delayed matching is related to the ventral frontal regions; and that successive, go/no-go tasks suffer most when orbitofrontal cortex is manipulated. What more general functions each of these subcategories of delay tasks represents is at present unclear and considerably more work is necessary to untangle the various variables that now confound interpretation of these nonetheless reliable results.

The analysis of delay tasks

Somewhat more headway has been made in understanding the functions represented by the general category of delay tasks. Such understanding may, of course, have to be revised when a clearer view is ob-

tained of the meaning of the subcategories. But, at the same time, elucidating the meaning of the subcategories may well depend on first understanding the overall problem.

Delay tasks, by definition, represent short-term memory processes: the subject is asked to perform on the basis of cues not present at the time performance is sought, but present some short interval (seconds to minutes) prior. But the locus of the disturbance produced in the short-term memory process by frontal lesions can be due to: (i) improper encoding of the cue — an attention and/or intentional deficiency; (ii) rapid decay of an encoded trace — a consolidation impairment; or (iii) confusion at the time of response — a retrieval deficit. Behavioral analysis has ruled out the trace-decay and retrieval deficit hypotheses (Pribram 1961), and this conclusion has been amply substantiated by the results of electrical stimulation of frontal eugranular cortex during the performance of delay tasks: the monkeys fail a trial when the stimulation to the frontal cortex occurs during the time of cue presentation and immediately (a few msec) thereafter (e.g., Stamm and Rosen 1973), but not when such stimulations are made during the delay period per se or at the time when response is demanded. Thus, the role of the frontal cortex in short-term memory has so far been shown to involve attention and encoding appropriate to the intended behavior, not trace decay or retrieval per se.

There is a good deal of additional evidence that *attention* to input (arousal) and *intention*, readiness or set to respond (activation) are both regulated by the frontolimbic formations of the forebrain. This evidence is the subject of a recent review (Pribram and McGuinness 1975) which identifies three separate but interacting frontolimbic systems. One system centers on the amygdala and deals with phasic *arousal* of the organism to novel, surprising input. A second system centers on the head of the caudate nucleus and related basal ganglia and tonically *activates* the brain, readying the organism for intended behavior. The third system centers on the hippocampus and coordinates arousal and activation, making it possible to maintain behavior in the face of distraction or to shift from one state of readiness to another without undue disruption.

It is tempting to relate the three frontal subsystems to these three frontolimbic mechanisms. As yet data have not been gathered with this aim in view. The hypotheses might therefore be fruitfully entertained that the orbital cortex is primarily related to the amygdala arousal system; the dorsal frontal cortex to the caudate readiness system; and the ventral frontal cortex to the hippocampal coordinating mechanism. The anatomical connections and physiological results obtained from stimulating these frontal subdivisions make the orbital and dorsolateral parts

of the proposal plausible (Kaada, Pribram and Epstein 1949, Pribram, Lennox and Dunsmore 1950, Pribram and McLean 1953 Nauta 1964). Behavioral results obtained from resections of the dorsal and the orbital areas also support the hypotheses (Pribram, Lim, Poppen and Bagshaw 1966, Rosvold 1972). With regard to the ventral frontal cortex, however, the effects on delayed matching from sample need to be tested with hippocampal resections. Other evidence (i.e., the fact that spatial delayed response remains unaffected by hippocampal lesions: Mishkin and Pri-

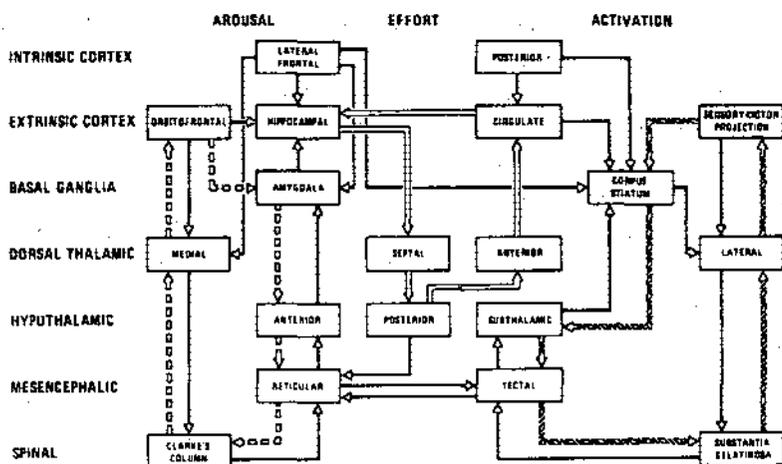


Fig. 2. Highly oversimplified diagram of the connections involved in the arousal (amygdala), activation (basal ganglia), and effort (hippocampal) circuits.

bram 1954) suggests that this correlation may not in fact occur. It is more likely that the known anatomical connections between the hippocampal system and the medial frontal and cingulate cortex (Pribram and Fulton 1954) will be the substrate of the arousal-activation coordinating system and that the ventral frontal cortex has yet another function related to the temporal isocortex with which this part of the frontal lobe is heavily connected (Mettler 1935, Bonin and Bailey 1947, Jones 1973). The temporal isocortex deals with selective attention (Rothblatt and Pribram 1972, Pribram, Day and Johnston, in press) via connections to the putamen, the remaining basal ganglion of the corpus striatum (Reitz and Pribram 1969, Buerger, Gross and Rocha-Miranda 1974). In short, the functions of ventral frontal cortex remain in doubt: they may relate to the hippocampal circuit, but are more likely to tie into a temporal lobe isocortex-putamen system which raises the unanswered question of the possible circuitry involved.

Distractibility

In recent years a few new facts have confirmed earlier findings and extended them. The new data concern two related domains: (i) the problem of orienting reactions to novel stimuli and therefore the organism's distractibility; and (ii) the importance of the frontal eugranular cortex in organizing sets or contexts that regulate the organism's behavior. Again, these domains can be conceptualized in terms of attention and intention, respectively.

First, frontal lobe resections interfere dramatically with the autonomic nervous system components of the orienting reaction. This effect of the lesion is coupled to an increased behavioral response to novelty — a failure to habituate to repetitions of a novel stimulus in both man and monkey (Luria, Pribram and Homskaya 1964, Pribram 1973; Grueninger and Grueninger 1973). The failure to habituate to an orienting stimulus is reflected in increased distractibility, which in monkeys is especially evident when spatial distractors — i.e., changes in the placement of cues — are involved (Grueninger and Pribram 1969). This finding suggests that, contrary to the more common interpretation, frontal resections influence the response to spatial cues by *disinhibition*, the common view being that dorsolateral frontal lesioned monkeys can no longer respond to spatial input. The more recent data suggest that the spatial input is responded to, but a failure in processing (ordinarily evidenced by habituation) is responsible for the observed deficit in behavior. For example, in a recently completed experiment (Brody 1975) monkeys were taught to press a panel next to another that was marked by being lighted green. Both normal and frontally lesioned monkeys learned to do this readily until the marked panel was shifted among 16 placements from trial to trial. Now only the normal monkeys were able to perform the task, the frontal-lobe-lesioned animals failing completely.

Taken together with the finding that interruption of the efferent connections of the frontal cortex are responsible for the lesion effects, the question is raised as to how the efferents work. Electrophysiological experiments by Lindsey and his students (especially Skinner) and Clemente and his group have traced inhibitory pathways in cat and monkey from frontal cortex, through midline diencephalic pathways to the mesencephalic reticular formation (Skinner and Lindsley 1973, Sauerland and Clemente 1973). The relationship needs now to be investigated between these pathways and the efferent connections from frontal cortex to the basal ganglia, spelled out via anatomical and behavioral techniques reviewed above. As noted, a separate neural system can be distinguished that deals with orienting (an arousal system centering on the

amygdala) which includes these fronto-diencephalic-reticular inhibitory pathways (Pribram and McGuinness 1975). Cutting the pathways or resecting the cortex of their origin ought to be disinhibiting and the behavioral result using spatial distractors is therefore in consonance with the electrophysiological data. According to this view, then, the distractibility due to frontal lesions is due to disinhibition of the ordinary control exercised by the frontal cortex.

Spatial context

In another set of experiments we tried to place the effects of frontal lesions in a somewhat more general framework. The delayed response test is similar in many respects to a task used to trace the development of intelligence in the infant by Piaget. In fact, delayed response was invented by Hunter at the University of Chicago shortly after World

TABLE I
Stages in the development of the object concept

Stage	Time (months)	Description
1 and 2	0-4	sucking reflexes; transient images; primary circular reactions
3	4-10	interrupted prehension; secondary circular reactions
4	10-12	coordination of secondary schemas; retrieval of hidden object
5	12-18	sequential displacements
6	18-24	invisible displacements

War I in order to determine whether children and animals could hold ideas in mind. In Piaget's work, the task is called an "object constancy" problem (Piaget 1954).

In a just completed study (Anderson, Hunt, Vander Stoep, and Pribram 1976) shows that frontally lesioned monkeys do in fact have difficulty when first faced with the object constancy task. In full view of the monkey a grape is hidden under one of three inverted baskets on a tray which is then pushed forward to allow the animal to lift the appropriate basket. This is a very rudimentary form of the delay task and I found many years ago that patients with ongoing pathology in frontal tissue (but not lobotomized patients) fail even this simple task.

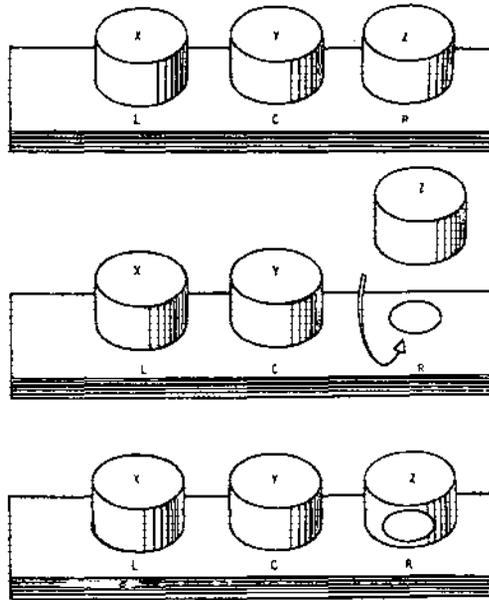


Fig. 3. Diagram showing delayed response type problem which illustrates Stage 4 of Piaget's object constancy paradigm.

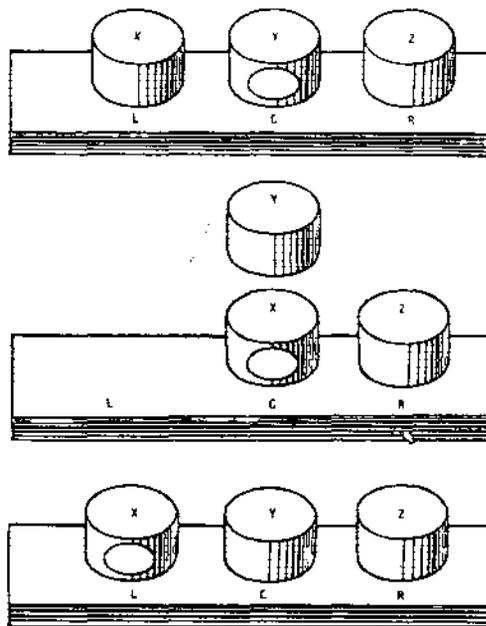


Fig. 4. Diagram showing delayed response type problem which illustrates context-dependency paradigm described in text.

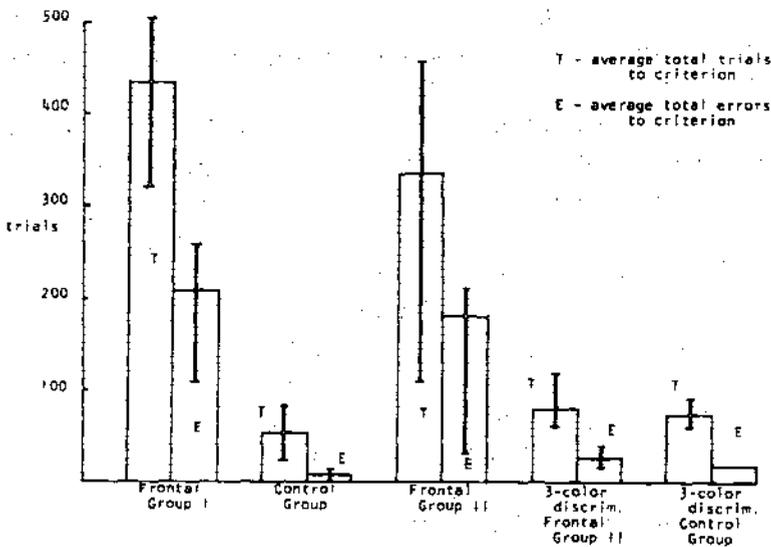


Fig. 5. Bar graph showing results obtained in the active search for vanished object problem (Piaget's Stage 4). Frontal Groups I and II were run in different orders to assure a balanced design.

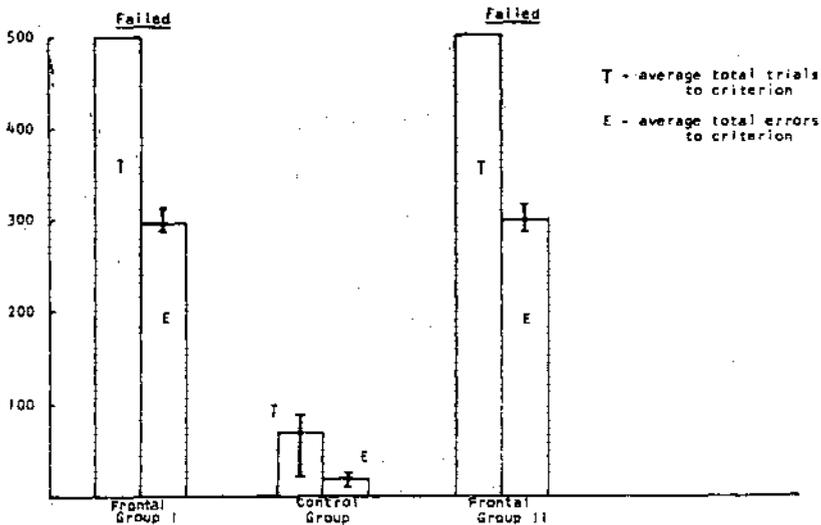


Fig. 6. Bar graph showing results obtained in the transient context modification problem. Frontal Group II is replication group for Frontal Group I, as noted in legend for Fig. 5.

But this is not the whole story. On the basis of some of the findings reviewed above, the hypothesis had been constructed that much of the difficulty experienced by monkey and man after frontal resections was due to a failure to develop appropriate sets or contexts within which behavior could become arranged. The object constancy-delayed response task (really the old-fashioned shell game) was therefore complicated so that the baskets were moved about (without lifting them) after the placement of the grape — all within view of the monkey. The baskets were conceived as the context within which the grape was hidden. Whereas the object-constancy problems (there was a series of them) were finally mastered by the frontally lesioned monkeys, albeit one (Stage 4) with a deficit, the context problems were *never* performed correctly — despite the fact that for normal monkeys these problems proved to be as easy as the object constancy versions.

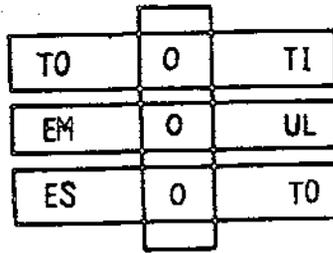
We initially interpreted these results as showing that two separate frontal lobe functions had been tapped by the experiment: one dealing with object constancy and the other with context processing. However, Bower has shown that the reason infants are defective in the object constancy situation is that they are distracted by the contextual cues within which the object becomes hidden (Bower 1972).

These results therefore again point to a disinhibiting role of frontal lesions which leave the organism more distractible. The results suggest additionally that distractibility interferes primarily with the establishment (perhaps by habituation) of a stable set or context within which novel stimuli (in this case spatial) can be processed, so that behavior can become appropriate to the situation at hand.

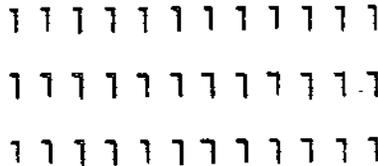
Temporal context

A final experimental result bears on this interpretation regarding the relationship between frontal eugranular cortex and the importance of context in determining appropriate perceptions and behavior. Warren McCulloch used to enjoy startling his audiences with readings (accompanied by sonorous intonations) and picturizations of the Marzy Doates (Mares eat oats) type:

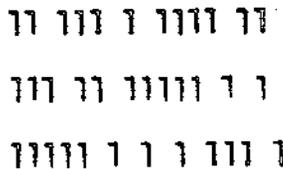
INMUDEELSARE
INCLAYNONEARE
INPINETARIS
INOAKNONEIS



were two of his favorites. I wondered whether, in the absence of an established context, the world of the frontal lobe lesioned monkey looked somewhat like the McCulloch presentations. In fact, I had devised a match task in 1946 to test just this possibility on lobotomized patients: instructions were given primarily non-verbally by showing the subject how to pick up the alternate match in regularly spaced series of three rows of twelve matches.



Then the following array was presented and the subject asked to do the same thing he had just done with the regularly spaced series:



Unfortunately I found that many control subjects as well as the lobotomized patients had difficulties in performing this task.

With monkeys the following test was devised as a modification of the delayed alternation procedure: Ordinarily the delay interval between responses is kept constant. A peanut or grape is alternately placed in one of two inverted baskets but not in view of the monkey. Thus the task goes: R (right basket) 5 sec, L (left basket) 5 sec, R 5 sec, L 5 sec, R 5 sec, etc. The modification entertained on the basis of McCulloch's readings was to alter the equal spacing of the delay period into an une-

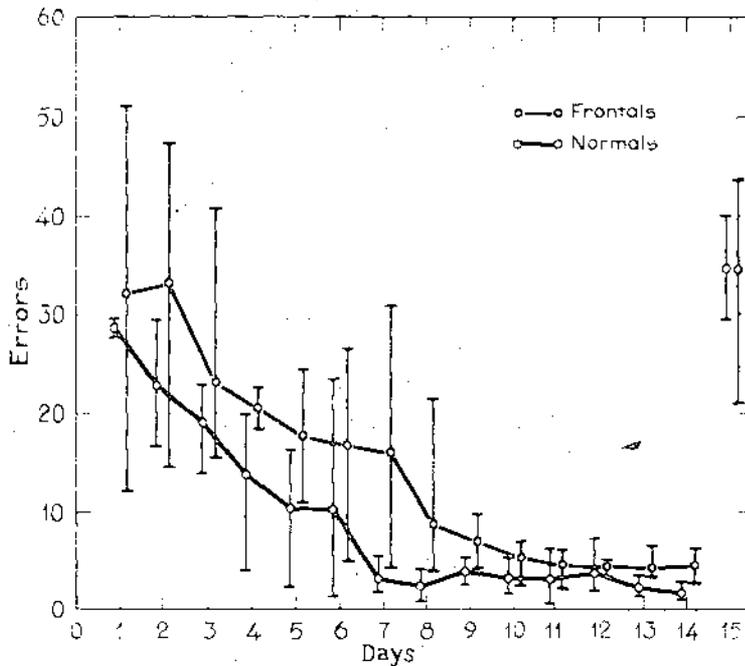


Fig. 7. Results obtained in the modified (5-15) alternation task referred to in text.

qual spacing: R 5 sec, L 15 sec, R 5 sec, L 15 sec, R 5 sec, etc. Behaving according to prediction, the frontal lobe lesioned monkeys failed the equal spaced task but were practically indistinguishable from unoperated controls in their performance of the unequally spaced task.

Milner (1971, 1974) has shown a somewhat similar effect for frontal patients using a test where "temporal tagging" (rather than the spatial "tagging" I had tried earlier) is used. A ready interpretation of these results would be that frontal lesions interfere with the temporal organization, the "parsing", of input so that it makes sense — becomes meaningful. A time tag, such as unequal spacing, would provide the necessary cues to parsing by the frontally lesioned subject which the normal organism ordinarily can supply to some extent himself.

In a just completed automated replication of the monkey experiment, a further control procedure was inserted. Each day the 5-15 spacing was reversed so that on Monday the monkey was tested on R 5 sec, L 15 sec, R 5 sec, L 15 sec, R 5 sec, etc., while on Tuesday the order would be R 15 sec, L 5 sec, R 15 sec, L 5 sec, R 15 sec, etc. Again, the frontally resected monkeys are performed essentially as did their unoperated controls (although they cannot maintain a criterion performance as readily as do the controls; see also Pribram, Konrad and Gainsburg,

1966) while doing considerably more poorly on the equally-spaced alternation task (K. H. Pribram, H. C. Plotkin, R. M. Anderson and D. Leong, in preparation).

For both the operated and unoperated monkeys, this version of the unequal interval alternation was extremely difficult. This, together with the results relating frontal cortex to spatial context already reviewed, raises the question as to whether temporal tagging is only one of several potent determiners of context. Another way of stating this question is to ask whether perhaps the frontal cortex is involved in the categorizing of relationships, much as the posterior intrinsic cortex is involved in the categorizing of properties. Of course, the possibility remains that different classes of categorization (e.g., temporal and spatial) are dependent on different portions of the frontal eugranular cortex and this possibility needs now to be tested.

In short, the current experimental results confirm and extend earlier ones in suggesting that the frontal eugranular cortex ordinarily serves to inhibit the distracting effects of novel inputs by processing the input (via habituation) in terms of an established context which controls what is attended and intended.

Conclusion: An hypothesis concerning frontal lobe function

The fashion today is to consider brain function in terms of information processing. Usually implicit in these formulations — though occasionally made explicit (e.g., as by Gibson 1966) — is the assumption that the information being processed “resides in” the *input* to the brain, and even in the *world* from which the senses derive their input.

The data on frontal lobe function reviewed here, while not denying the importance of input, do focus our attention on a currently neglected aspect of brain function — its spontaneous activity, its generative capacities. True enough, the spontaneous neural rhythms become initially programmed by input (unless the programs are pre-established, i.e., innately given) but they are then maintained as central states by memory mechanisms that serve as the context within which subsequent input becomes processed. Our search for the routes taken by information processing need not, therefore, necessarily come up with an input→central processor→output paradigm. Rather, as demonstrated here for frontal lobe function, and elsewhere (Pribram 1971, 1974) for other parts of the brain, a more practical and realistic paradigm is:

central processor $\begin{matrix} \leftarrow \text{input} \\ \rightarrow \text{output} \end{matrix}$

The emphasis in this paradigm becomes the organization of central brain states which control input and output rather than the transmission of signals from receptors to effectors. The change in view is comparable to that in chemistry where analysis of simple one-way reactions gave way to the analysis of reciprocally interacting thermodynamic systems. We must therefore begin to analyze neural function in terms of variables (e.g., time constants) similar to rate-limiting reactions studied by biochemists. We need to understand neural inhibition as an organizing process, not one which necessarily leads to the inhibition of perception and behavior: as described here, the neural disinhibition resulting from frontal lesions results in perceptual and behavioral disorganization (disruption of context) which in the same animal can be manifested as increased distractibility (behavior disinhibition) or perseveration (behavioral inhibition), depending on the situation in which the monkey is being studied (Pribram, Ahumada, Hartog and Roos 1964). Thus the task ahead is to formulate currently feasible neurophysiological experiments which detail the mechanisms by which frontal cortex organizes the context — categorizes the relationships — within which behavior occurs.

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