T-2

# TOWARD A SCIENCE OF NEUROPSYCHOLOGY

## (*Method and Data*)

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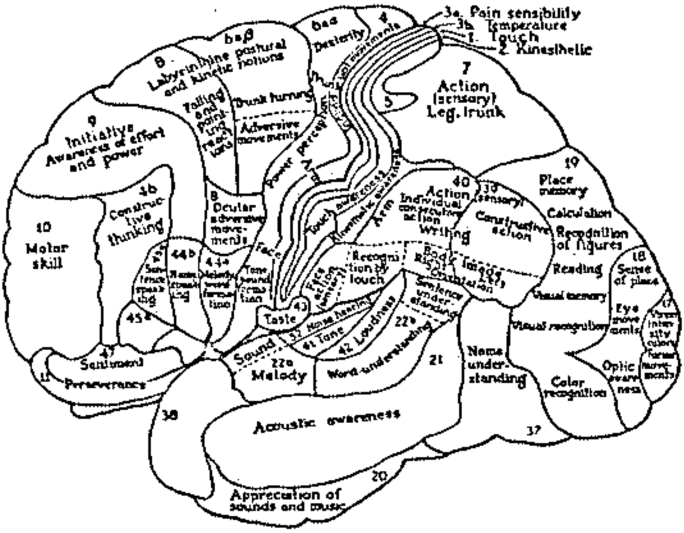
DR. PATTON asked me to discuss with you the relationship between neurophysiology and psychology. With the increasing popularity of the "interdisciplinary approach" there would be no apologia necessary for a science of neuropsychology were it not for the bad repute into which this area of investigation has fallen. Such well-deserved infamy stems, in part, from the dualism which has plagued all of the behavioral sciences during the past 50 years and, in part, from the *excessive* "psychologizing" of physiologists and "physiologizing" of psychologists which fills our journals and monographs. The first figure serves to illustrate the results of such schizoid endeavors.

The deficiencies of the conceptualizations diagramed here become obvious once they have been pointed out. What psychophysicist would assign the same numeral to different classes or assign different numerals to the same class? Yet, flagrant disregard of this simple rule of the most elementary of scaling techniques pervades practically every cytoarchitectonic study and is shown at its worst in Figure 1. What biologist would, in his own field, classify together such diverse categories as ocular adversive movements, optic awareness, vision intensity, color recognition, place memory, constructive thinking, and constructive action, without some



LOCALIZATION OF THE FUNCTIONS OF THE CEREBRAL CORTEX ON ANATOMIC LINES. OUTER SURFACE
From Kleist. K: Kriegsverletzungen des Gehirns. p 1365.

FIGURE 1. "Localization of function" in the human brain according to a recent authority. See text for "what's wrong" with this figure.

referent of internal consistency and some attempt at ordinal ranking? Finally, where is there available a discussion of the reliability and the validity of the techniques used to construct this monstrosity? The vast differences between various textbook diagrams and the differences between these and our clinical experience suggest the answer to this question.

But what of the experimental studies which have dealt with the relation of brain and behavior? Many such studies using behavioral measures have manipulated environmental conditions and inferred brain function. Other studies have manipulated the central nervous system and measured electrical, histological, or physiological (e.g., movement, blood pressure) responses and inferred a relationship to behavior. Such inferences appear to suffer from the paucity of data accumulated thus far. Some studies have manipulated the brain and measured behavior; these often suffer from the limited applicability of the specific findings. In an attempt to overcome these difficulties, the type of study reported here was undertaken: In these experiments *both* the central nervous system *and* environmental conditions were manipulated and the interaction of these manipulations with the behavior of the organism has been measured.

Since this approach is still in its infancy, data rather than laws will be presented. The data describe the relationships between the manipulations performed (independent variables) and behavior (the dependent variable); it seems premature to attempt systematization of the interrelationships of these independent and dependent variables and thus to formulate laws or concepts. When such laws are formulated, they will, of necessity, be within the framework of a behavioristic psychology. The problem of relating such scientific laws to "private experience" (or Gestaltists' "phenomena") is a problem which behavioristic psychology shares with other sciences and lies beyond the scope of this conference.

Since this approach considers the biology of the organism as one of several classes of independent variables determining behavior, a necessary first step toward a science of neuropsychology (by definition, a reductive science) is a description of the central nervous system in terms other than those defining relationships to the dependent variable (behavior) used in the neuropsychological experiments. Such description is the task of neuroanatomy and classical neurophysiology. For this occasion, I have chosen a description based on thalamocortical anatomy, though one based on cytoarchitecture, "evoked potential" studies, strychnine "neuronography," or a combination of these might have served as well.

Thalamocortical systems may be classified according to whether the thalamic component receives its major afferents from within or from outside the thalamus. The term "intrinsic" has been applied by Rose and Woolsey[17] to those thalamic nuclei which do not receive their major afferents from outside the thalamus. Thalamocortical systems receiving extrathalamic afferents are of two types: those receiving spinal and mesencephalic afferents, and those receiving diencephalic fibers. The former (often called the "primary projection systems") are hereinafter called "extrinsic," following Rose and Woolsey; the latter are most usefully considered under the heading "rhinencephalic."[11] Two examples of current investigation of the intrinsic systems and one example of those of the rhinencephalic systems will be presented.

Figure 2 presents the surgical manipulations of the neural variable in these experiments. Represented are the reconstructions of the cerebral hemispheres of 40 monkeys. The lesions were made, in most instances, on the basis of criteria other than those defining the thalamocortical relationship, a consideration which need not enter this presentation. All diagrams are made by transferring to standard brain outlines the actual

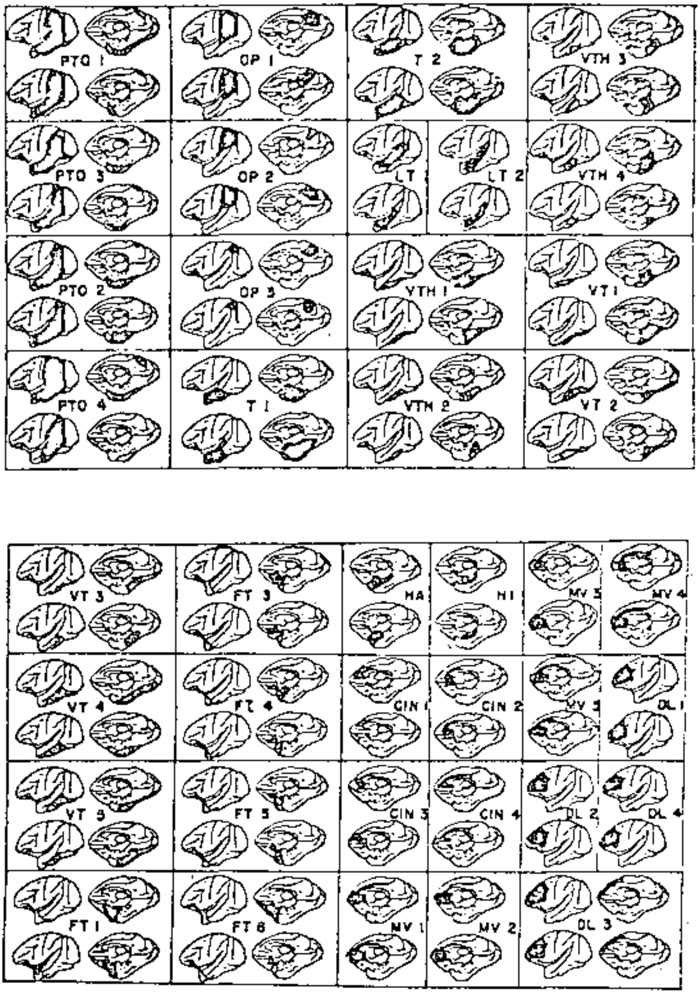


FIGURE 2. Schematic representation of locus and extent of resections performed in 40 monkeys used to relate specific neural systems to specific behavioral processes. (The original reconstructions of the brains of these animals appear in References 5, 6, 8, 9, 10, 14.)

reconstructions from serial sections of the lesioned hemispheres.

In order to decide upon a relevant dependent vari-

SIMULTANEOUS VISUAL CHOICE REACTION

| Operates Without Deficit | Pre | Post |
|---|---|---|
| OP 1 | 200 | 0 |
| OP 2 | 220 | 0 |
| OP 3 | 380 | 0 |
| LT 1 | 390 | 190 |
| LT 2 | 300 | 150 |
| H 1 | 210 | 220 |
| HA | 350 | 240 |
| FT 1 | 580 | 50 |
| FT 3 | 50 | 0 |
| FT 4 | 205 | 0 |
| FT 5 | 300 | 200 |
| FT 6 | 250 | 100 |
| DL 1 | 160 | 140 |
| DL 2 | 540 | 150 |
| DL 3 | 300 | 240 |
| 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 |

| Operates With Deficit | Pre | Post |
|---|---|---|
| PTO 1 | 120 | 272 |
| PTO 2 | 325 | F |
| PTO 3 | 180 | F |
| PTO 4 | 120 | 450 |
| T 1 | 940 | F |
| T 2 | 330 | F |
| VTH 1 | 320 | F |
| VTH 2 | 370 | F |
| VTH 3 | 280 | F |
| VTH 4 | 440 | F |
| VT 1 | 240 | F |
| VT 2 | 200 | F |
| VT 3 | 200 | 890 |
| VT 4 | 410 | F |
| VT 5 | 210 | F |

| Non-Operate Controls | | |
|---|---|---|
| C 1 | 790 | 80 |
| C 2 | 230 | 20 |
| C 3 | 750 | 20 |
| C 4 | 440 | 0 |

FIGURE 3. Pre- and postoperative scores on a simultaneous visual choice reaction of the animals whose brains are diagramed in Figure 2 indicating the number of trials taken to reach a criterion of 90 per cent 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 over-all results as given in the text and in the following figures.)

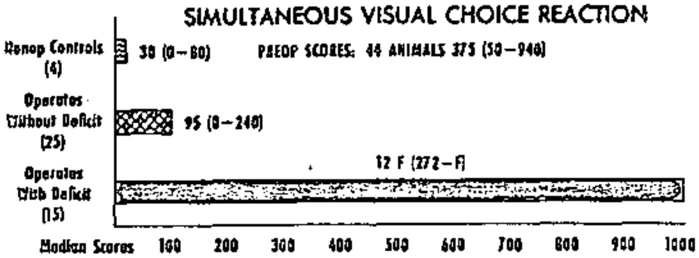
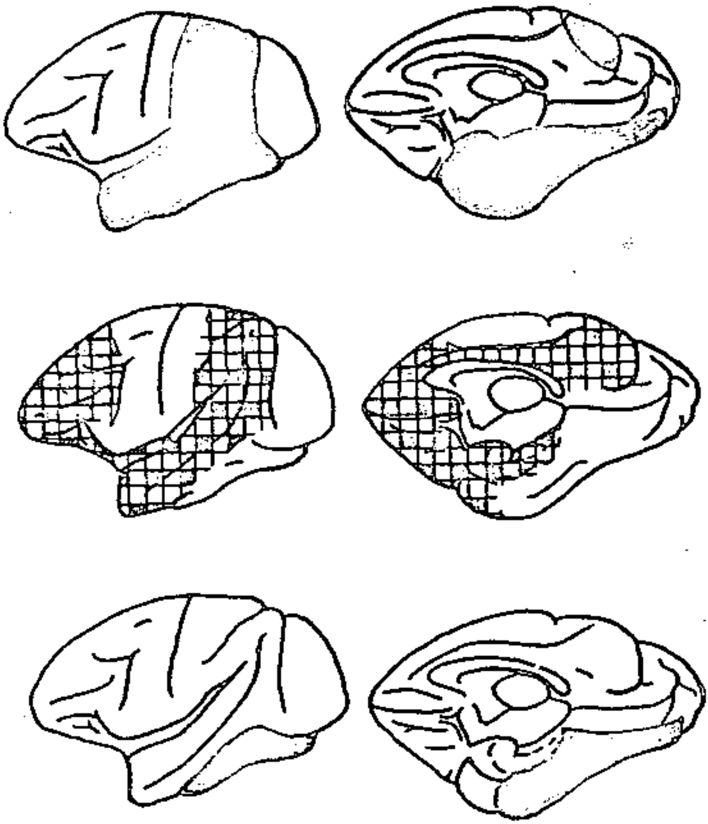


FIGURE 4. Bar graph of median scores of the groups delineated in Figure 3. The number of animals per group is indicated below group name; the range from which median scores are taken appears in parentheses next to the median.

able, approximately 30 different behaviors were observed and quantified. Those behaviors which were affected by some lesions and not by others were then chosen for further investigation. Our first example of such behavior is the visual choice reaction or visual discrimination task.

Figure 3 gives the individual animal's pre- and postoperative scores in a visual choice reaction in which painted patterns were used as cues. Figure 4 summarizes these results. Scores were classified into deficit and no-deficit on the basis of whether an animal took longer to relearn the task postoperatively than to learn it preoperatively. As can be seen, there is no overlap in scores between the group with no-deficit and that with deficit; in fact, the latter group contains 12 of 15 animals which *never* relearned the task even though 1,000 trials were given postoperatively (preoperative mean for learning was approximately 375).

Figure 5 groups the lesions of the animals with deficit and those without deficit. *A* shows the summed area of



VISUAL CHOICE REACTION

FIGURE 5. The upper diagram *A* represents the sum of the areas of resection of all of the animals grouped as showing a deficit in Figure 3 and Figure 4. The middle diagram *B* represents the sum of the areas of resection of all of the animals grouped as showing no-deficit in Figure 3 and Figure 4. The lower diagram *C* represents the intersect of the area shown in black in the upper diagram and that *not* checkerboarded in the middle diagram. This intersect represents the area invariably implicated in visual choice behavior in these experiments.

all of the lesions which produced deficit; *B* the sum of the area of all of the lesions which failed to produce a deficit in visual discrimination performance. *C* represents the intersect of the area shown in *A* with the total area *not* shown (checkerboarded) in *B*. This may be considered an approximate minimal locus implicated in visual choice behavior in the 40 lesioned animals. This locus approximates that of one of the posterior intrinsic systems and will be referred to as the "inferotemporal" sector.

Having established a selective relationship between a lesion in one of the intrinsic systems and a restricted portion of the behavioral spectrum, we proceed to investigate the environmental conditions upon which this relationship is dependent. For instance, we have called the task a visual choice reaction. Is performance of other visual discriminations affected by this lesion? So far, experiments have shown performance of a variety of visual object, color, and brightness discriminations to be altered.[5,6] What would happen if in place of the visual discriminanda, their logical analogues in somesthesis were substituted? Would the same, or a different, cortical area be implicated?

Figure 6 shows the results of an experiment where the visual choice reaction was compared with a task in which vision was excluded and a solution of the problem depended on *handling* the cues. Two intrinsic systems were surgically invaded—the inferotemporal and the occipitoparietal. As can be seen, lesions of the occipitoparietal sector fail to interfere with visual choices but affect those based on somethesis, whereas the lesions involving the inferotemporal sector interfered selectively with the visual.[8]

FURTHER BEHAVIORAL ANALYSIS
OF THE PTO CORTEX

| | P48 | P46 | P49 | T44 | T45 |
|---|---|---|---|---|---|
| Visual | | | | | |
| 10 (0-70) | 0 | 0 | 0 | (500) | (500) |
| Somatosensory | | | | | |
| 60 (0-100) | 460 | 120 | 350 | 70 | 50 |
| New Somatosensory | (1000) | (1000) | (1000) | 320 | 260 |

FIGURE 6. Comparison of retention scores of inferotemporal *T* and occipitoparietal *P* operates on a visual and somesthetic task in which logically analogous cues (+ vs. 0) were used. The mean and range of the preoperative retention scores appear under the title of the task. The scores on the "new somatosensory" task indicate original postoperative learning of a length discrimination. Parentheses indicate *failure* to reach criterion in the number of trials given.[9]

If it can be stated that the decrement in performance is restricted to the visual choice reaction, and other experiments on taste,[1] conditioned avoidance,[15] and delayed response[2, 6, 9, 10, 14] support this contention, we are faced with a second cerebral "visual" system. Thus, in addition to the extrinsic (geniculo-striate) system, there is at least one intrinsic system which functions selectively within this modality. It becomes important, therefore, to distinguish between the functions of the extrinsic and intrinsic visual systems. For example, resections within the former, that is, of the striate cortex, lead to field defects; those of the latter, the inferotemporal cortex, do not. Other studies which specify such differences have been completed or are in progress and will be reported elsewhere.[8, 19]

Today, I wish to limit myself to one other aspect of the relationship of inferotemporal lesions to visual choice behavior.[13] Figure 7 describes an experiment in which animals were taught to choose one of two discriminanda (an ashtray and a tobacco tin) presented simultaneously. The animals were then tested in situations in which these identical cues were presented successively, and the performance of inferotemporal operates was compared with that of control operate and non-operate control groups. Here, as in the experiments of Riopelle and Ades,[16] and of Mishkin,[5] infero-

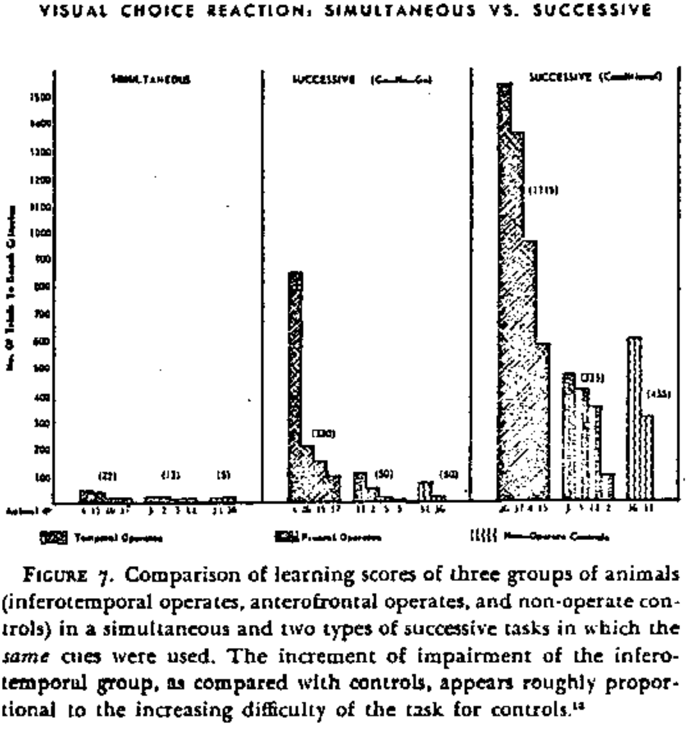


FIGURE 7. Comparison of learning scores of three groups of animals (inferotemporal operates, anterofrontal operates, and non-operate controls) in a simultaneous and two types of successive tasks in which the *same* cues were used. The increment of impairment of the inferotemporal group, as compared with controls, appears roughly proportional to the increasing difficulty of the task for controls.[14]

temporal operates have progressively greater difficulty in a series of tasks graded in "distinctiveness" as measured by the difficulty of the task for the control groups. In this instance, however, "distinctiveness" is not dependent on the physical dimensions of the cue, but

CLASSICAL DELAYED REACTION

| Operates Without Deficit | | | Operates With Deficit | | |
|---|---|---|---|---|---|
| | Pre | Post | | Pre | Post |
| PTO 1 | 680 | 270 | DL 1 | 290 | F |
| PTO 4 | 1020 | 540 | DL 2 | 210 | F |
| T 2 | 670 | 120 | DL 3 | 590 | F |
| VTH 1 | 100 | 0 | DL 4 | 240 | F |
| VTH 2 | 60 | 0 | MV 2 | 610 | 960 |
| VTH 3 | 560 | 0 | MV 3 | 430 | 750 |
| VT 1 | 290 | 20 | | | |
| VT 2 | 130 | 0 | | | |
| VT 3 | 740 | 330 | PTO 3 | 530 | 630 |
| LT 1 | 140 | 0 | T 1 | 60 | 90 |
| LT 2 | 140 | 0 | | | |
| H 1 | 350 | 50 | | | |
| HA | 170 | 140 | | | |
| FT 3 | 200 | 100 | | | |
| FT 4 | 300 | 0 | | | |
| FT 5 | 750 | 300 | | | |
| FT 6 | 1250 | 400 | | | |
| CIN 1 | 820 | 360 | | | |
| CIN 2 | 600 | 150 | Non-Operate Controls | | |
| CIN 3 | 215 | 150 | C 1 | 10 | 110 |
| CIN 4 | 345 | 180 | C 2 | 590 | 0 |
| MV 1 | 630 | 60 | C 3 | 230 | 250 |
| MV 4 | 590 | 240 | C 4 | 440 | 330 |
| MV 5 | 380 | 230 | | | |

FIGURE 8. Pre- and postoperative scores on delayed reaction of animals whose brains are diagramed in Figure 2, indicating the number of trials taken to reach a criterion of 90 per cent on 100 consecutive trials. Deficit is defined as a larger number of trials taken in the "retention" test than in original learning.

rather on the situation in which these cues are imbedded. Thus, no selective relationship between the visual discrimination impairment and either of these two classes of environmental variables (cue dimension, situation) is established. I believe this lack of a simple relationship between the physical dimensions of cues and the performance of monkeys with inferotemporal lesions will differentiate these results from those obtained when the extrinsic (geniculo-striate) visual system is invaded. Thus, the distinction between such concepts as "agnosia" (which might account for the results of the "situational" experiment) and "acuity loss" (which might account for the results found on varying the physical dimensions of the discriminanda), which have been traditionally employed to explain the disparate effects of lesions in the extrinsic and intrinsic systems, may be revised in more precise terms allowing interdisciplinary translation.

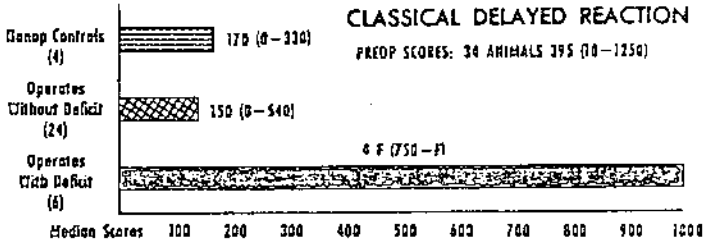


Figure 9. Bar graph of median scores of the groups delineated in Figure 8. The number of animals per group is indicated below the group name; the range from which median scores are taken appears in parentheses next to the median.

A *second* example of this approach to the functions of the intrinsic systems is presented in Figure 8 which

DELAYED REACTION

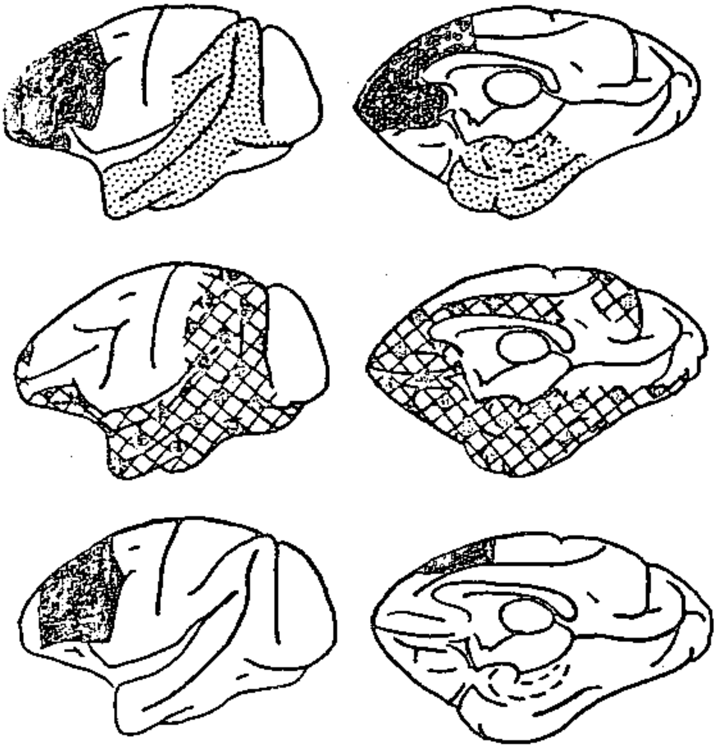


FIGURE 10. The upper diagram *A* represents the sum of the areas of resection of all of the animals grouped as showing a deficit in Figure 8 and Figure 9. The middle diagram *B* represents the sum of the areas of resection of all of the animals grouped as showing no-deficit in Figure 8 and Figure 9. The lower diagram C represents the intersect of the area shown in the upper diagram and that *not* checkerboarded in the middle diagram. This intersect represents the area invariably implicated in delayed reaction performance in these experiments. (Note that resections within the area stippled in the upper diagram occasionally result in "deficit" as defined here. However, note also, that a similar "deficit" appears in the non-operate controls in Figure 8.

This finding resolves the discrepancies regarding previously described occasional occurrence of deficit on delayed reaction following posterior cortical resections.[5,6] For the purposes of a "localization" procedure, the delayed alternation task appears to be more reliably retained. Nevertheless, as demonstrated here, the results of delayed reaction experiments may still be useful.)

shows the scores in the delayed reaction made by the animals with the lesions presented in Figure 2. Figure 9 summarizes these data on the basis of animals with and without deficits defined in the same way as in the case of visual choice reaction. Figure 10 shows in *A* the sum of the area of the lesions of the animals with deficit and in *B* the sum of the area of the lesions of the animals without deficit; *C* shows the intersect of area *A* and the area *not* included in *B*. This area corresponds roughly to another intrinsic system, the anterofrontal sector. We are, thus, ready to investigate another of the intrinsic cerebral systems.

The delayed reaction may be manipulated in a manner similar to that which we used in the visual choice reaction. Figures 11 and 12 present the results of such manipulations.[7] *A* shows the difference in performance between animals with anterofrontal resections and control operates in the traditional delayed reaction. In this task the animal chooses the cup containing a peanut from one of two identical cups, on the basis of a cue presented sometime prior to opportunity for response. This cue is not present during the delay period or at the time of response. *B* shows that (1) when the predelay cue is varied from showing a peanut (or object) to the right or to the left of the animal to showing a peanut or a bare hand (or two distinct objects), and (2) when the conditions of response are varied to oppor-

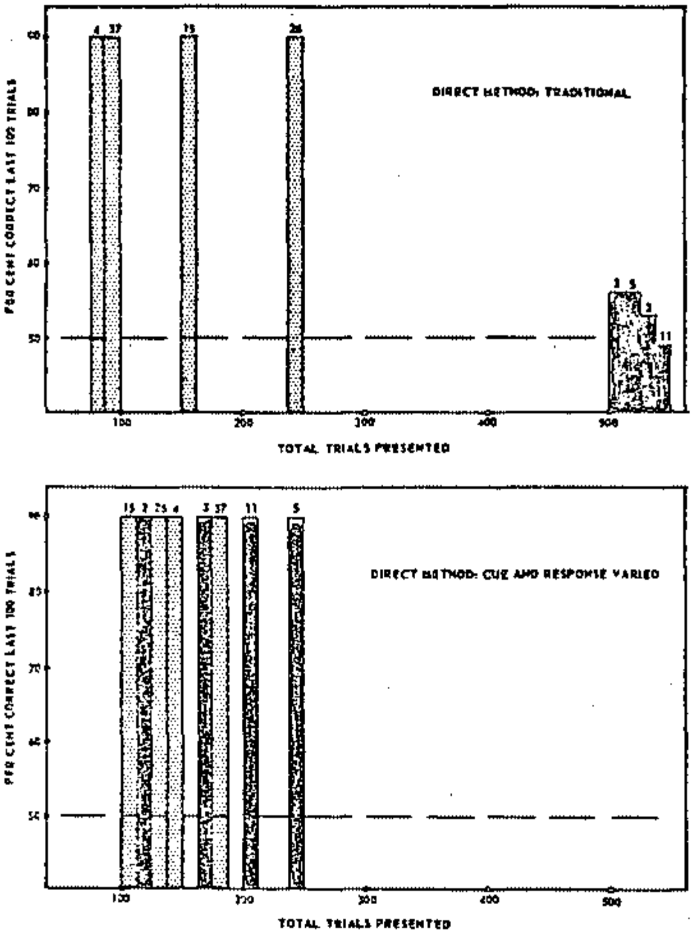


FIGURE 11. Bar graph comparing the performance of anterofrontal and control (inferotemporal) operates on two types of delayed reaction. Each bar represents the performance of one animal (designated by the number above the bar). Note the successful performance of anterofrontal operates (comparable with that of controls) when the method of presentation of predelay cues and opportunity for response are both changed from a simultaneous, right-left situation (upper diagram) to a successive, go—no go situation (lower diagram).[7]

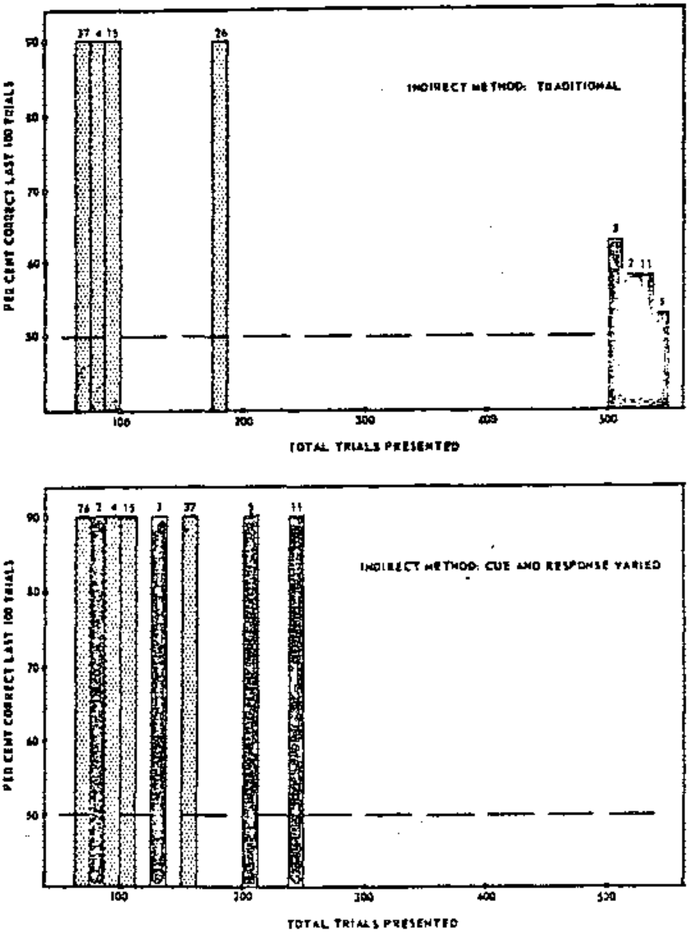


FIGURE 12. Same as Figure 11 except that the indirect method of cueing was used. Results are comparable to those obtained when peanuts are used (direct method).[7]

tunity for opening or not opening a single centered cup, animals with frontal lesions perform almost as well as their controls. When either the predelay cues or response conditions are varied alone, such dramatic improvement of frontal operates' performance does not take place. However, as can be seen from Figure 13, manipulations of the predelay cue are markedly more effective than manipulations of the response conditions. In these experiments when the predelay cue was changed from a spatial to a non-spatial one, frontal operates' performance improved. This might have been the result of changes in the spatial aspect of the discriminans. On the other hand, the relevant change might be the fact that for monkeys the peanuts and objects used as predelay cues had acquired greater "distinctiveness" during prior testing than is possible with a right-left choice. Comparing performance on another task, spatial alternation, which is also consistently failed by anterofrontal operates, with these animals' performance in a non-spatial object alternation, should answer the question of whether spatiality or "acquired distinctiveness" of cues is the relevant variable accounting for the improved performance of the above tasks. Figure 14 compares performance in 1,000 trials of anterofrontal operates and control operates in spatial and object alternation.[12] As can be seen, frontal operates *are* impaired in their performance of both tasks. Thus, spatiality per se cannot be the relevant predelay cue dimension responsible for anterofrontal operates' failure in delayed-response type tasks. Rather, the result of this experiment suggests the hypothesis that the remarkably high level of performance achieved by frontal operates on certain variations of delayed response are due to the "distinctiveness" which the pre-

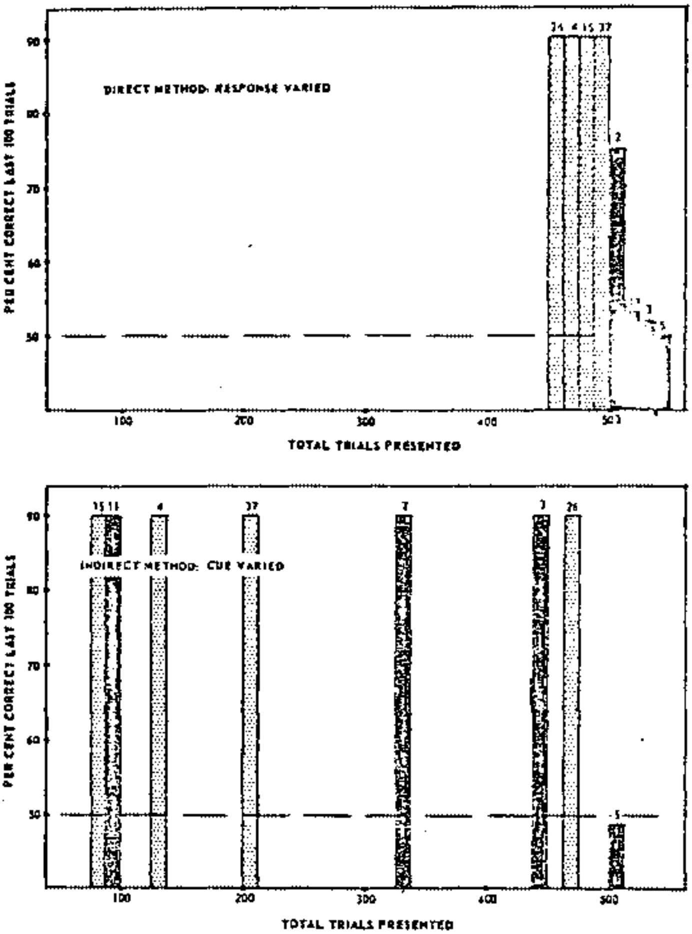


FIGURE 13. Bar graph comparing the performance of anterofrontal and control (inferotemporal) operates on further variations of the delayed reaction task. The upper graph represents performance when cues are presented in right-left positions as in the classical method but opportunity for response is go—no go as in the successive method. The lower diagram represents performance when cues are presented successively but opportunity for response is unchanged from that used in the classical method (go right—go left).[7]

delay cues had acquired during prior training. Conversely, performance decrement, when present in such animals, must be considered a function of the distinctiveness of the predelay cue. Thus, frontal operates' impairment on classical delayed response is a function, not only of the delay, but also of the distinctiveness of the predelay cue.

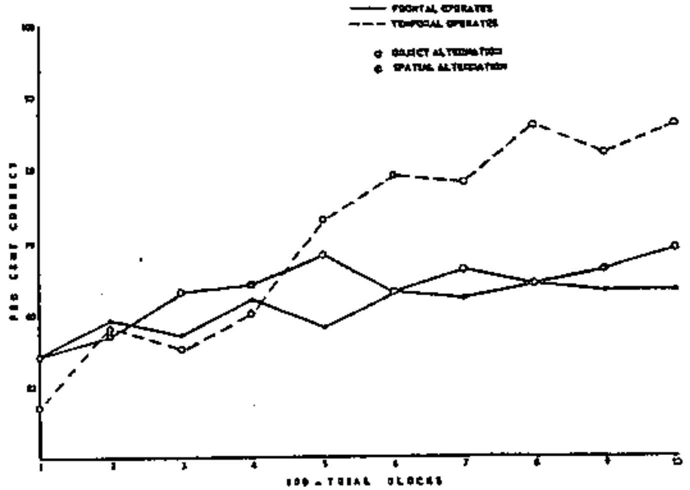


FIGURE 14. Performance curves of anterofrontal and control operates on spatial and object alternation. Note that anterofrontal operates are equally impaired in the performance of both tasks. On spatial alternation temporal operates achieved a 90 per cent level of performance within 250 trials.[12]

The impairment in choice behavior which follows lesions of both intrinsic systems discussed is, therefore, a function of distinctiveness of cues. The effects of resection of the posterior (inferotemporal) system and the anterior (anterofrontal) are *distinguished* in terms of other relevant variables: The posterior system has been related to discrimination behavior which is modality specific; the anterior system to discriminations made in the presence of a temporal gap between cue presentation and response.

At this point I should like to turn from the intrinsic systems. Since one of the functions of this symposium is to discuss the relation of all of the behavioral sciences, the following experiment is apropos. In this instance, the surgical manipulation involved a portion of the second rhinencephalic system,[18] the amygdaloid complex of the cerebral hemisphere. The environmental manipulation concerned a social group of eight preadolescent male macaques. A dominance ranking of each animal with respect to other animals in the group (during feeding) was obtained prior to surgery. Figure 15 demonstrates this preoperative hierarchy. Figures 16, 17, and 18 show the effect on this hierarchy of bilateral amygdalectomy of the three most dominant animals (one animal operated on at a time). Although all lesions are of comparable extent, there are differences among the operates in direction and degree of change in social behavior. Thus, Dave drops from the #1 position to become #8; Zeke, who became the dominant animal after Dave's demise, was also sent downward in the hierarchy by the resection. Riva, Zeke's successor, however, met with no such fate. On the basis of this and subsequent experiments in which relevant variables were manipulated separately, it appears that the amount of aggressive behavior displayed by the #2 animal toward the operate during the immediate postoperative period may be critical in determining the effect of amygdalectomy. Thus, as in the case of the intrinsic systems, complete description of the effects

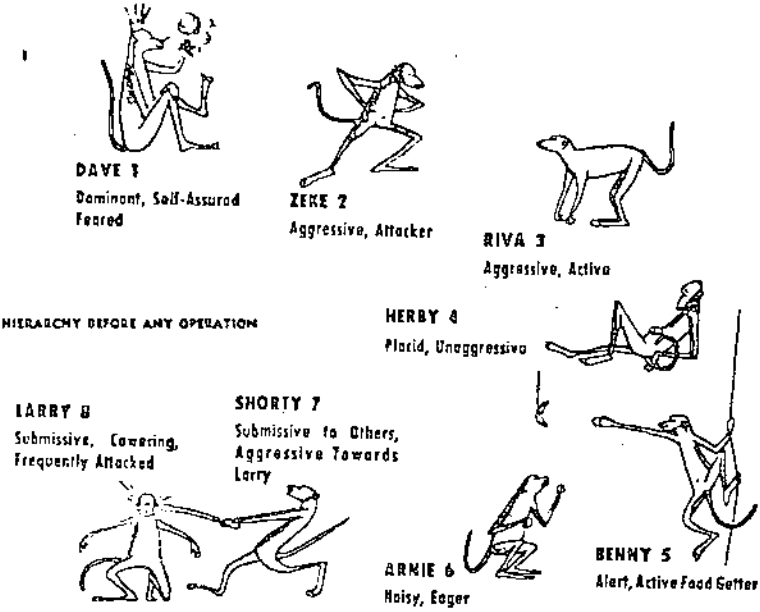


FIGURE 15. Dominance hierarchy of a colony of eight preadolescent male rhesus monkeys before any surgical intervention.[19]

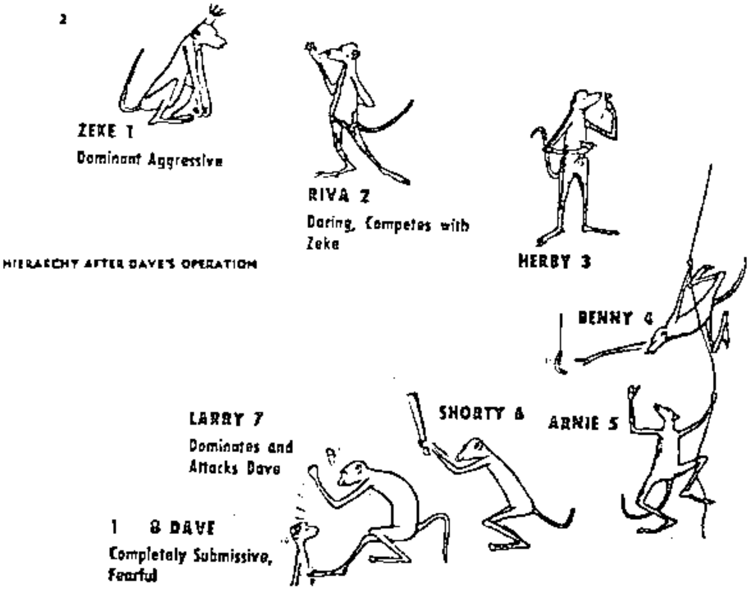


FIGURE 16. Same as Figure 15 after bilateral amygdalectomy had been performed on Dave. Note his drop to the bottom of the hierarchy.

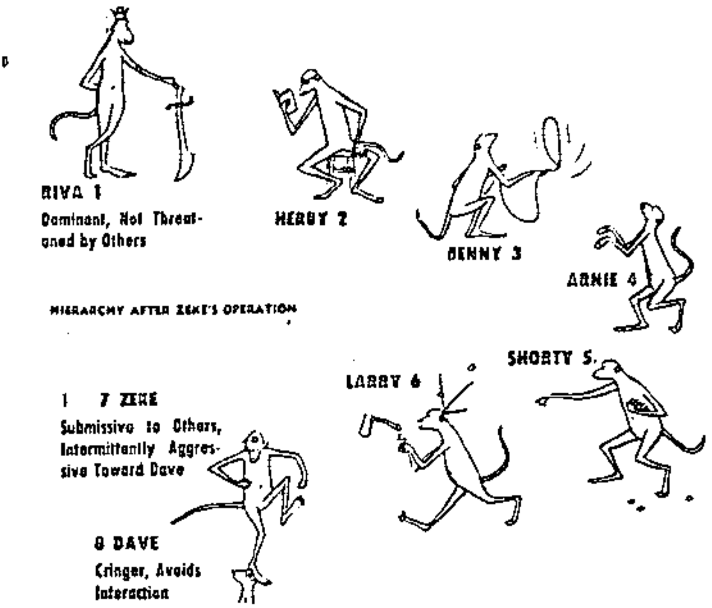


FIGURE 17. Same as Figure 15 and Figure 16 except that both Dave and Zeke have received bilateral amygdalectomies.

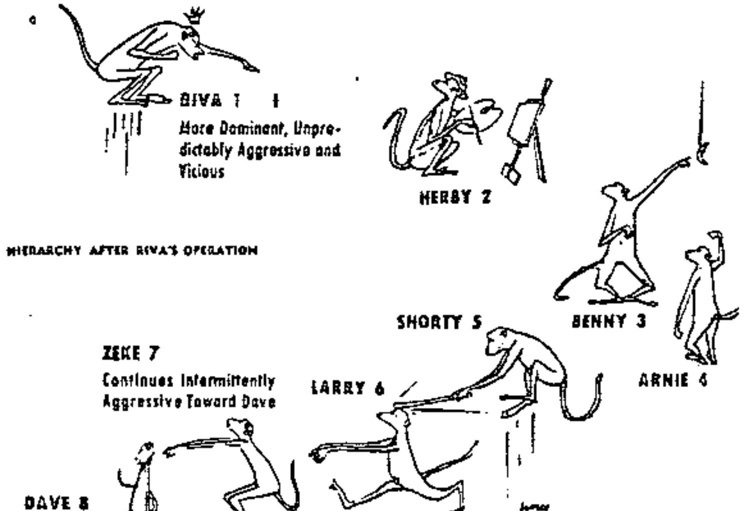


FIGURE 18. Final social hierarchy after Dave, Zeke, and Riva have all had bilateral amygdalectomies. Minimal differences in extent and locus of the resections do not correlate with differences in the behavioral results. As noted in the text, Herby's nonaggressive "personality" in the #2 position of the hierarchy seems the most likely explanation of the disparate effects of similar lesions.[18]

of brain lesions *must* include specification of the environmental variables which determine the changes in behavior.

*In Summary:* As indicated in the title of this presentation, I have discussed method and data (relations between dependent and independent variables) which may lead toward a science of neuropsychology. Conspicuously undeveloped are the laws (relationships to a dependent variable of classes of interrelated independent variables) which form the substance of any science. I feel, perhaps erroneously, that there is, as yet, an insufficient scope of data to allow the formulation of general laws. However, some of the terms which must be included in any rigorous formulation are being uncovered.

As an example, some cerebral systems have been surgically manipulated on the basis of neuroanatomical and neurophysiological data and some relationships to behavior have been described. The cortex of these systems has previously been referred to as "associative" on the basis of presumed anatomical connections, physiological "silence," and "clinical" observation. The experiments described offer one method of delineating more precisely the role of these systems in behavior. The inferotemporal sector has been selectively related to performance of visual choice reactions. Resections of this sector result in impairment of visual choice reactions, the impairment being proportional to the distinctiveness of the discrimination as defined by the difficulty of the task for control animals. The dimension of "distinctiveness" is related not only to the physical parameters of the cue, but also to some "non-cue" (situational) variables determining the response.

A second example concerned the relationship of the anterofrontal sector to choice behavior dependent on cues not present at the time of response. Experiments have been reviewed which show that this relationship is insufficiently described by the parameter of temporal contiguity between pre- and postdelay contingencies, and that "distinctiveness" of the predelay cue is as important a variable as "time." Thus, the effects of lesions of both intrinsic systems discussed are a function of the distinctiveness of the cues upon which the choice behavior is dependent. The effects of lesions of the posterior and anterior systems may be distinguished, however, by other relevant variables: The posterior lesion has an effect which is modality specific; the anterior lesion is effective only when choice is dependent on cues temporally remote from the response.

The third example concerned one of the rhinencephalic systems and showed that specification and manipulation of environmental variables is as important in understanding the relation between brain and social-emotional behavior as in understanding such a relationship to choice behavior. The example showed that comparable lesions of the amygdaloid complex resulted in diverse effects on the dominance of a #1 animal in a social hierarchy depending on the amount of aggressive interaction with the #2 animal during the immediate postoperative period.

Accumulation of data according to the approach presented here should make possible, in the future, a systematization of relationships between neurological and behavioral data which will constitute a science of neuropsychology. Though the development of this science is dependent on the development of neurology and psychology, the reductive sibling may be expected to add impetus to the growth of its less hybrid sister sciences. At present, data gathering, guided by hypotheses, fills our time and capacity. It is my hope that the results of these endeavors may stimulate others to join in this approach, for, only when data sufficient in range and scope are available, will the formulations which constitute a science be possible. Our particular science, neuropsychology, has a special role to fill at this time: The largest gap in our conceptualizations lies between the behavioral and the physiological sciences —a gap paralleling that which existed between the physiological and physical sciences a century ago. A common framework for the physical and physiological sciences resulted from experiments such as the synthesis of urea—from neuropsychological experiments we may expect the emergence of a common framework relating physiological and behavioral science.

## REFERENCES

1. Bagshaw, M. H. and Pribram, K. H. Cortical organization in gustation (macaca mulatta). *J. Neurophysiol.*, 1953, 16:499-508.
2. Blum, J. S., Chow, K. L., and Pribram, K. H. A behavioral analysis of the organization of the parieto-temporal-preoccipital cortex. *J. comp. Neurol.*, 1950, 93:53-100.
3. Gunter, R. The effect of resection of the striate cortex and of the inferotemporal cortex on a visual brightness discrimination. (In preparation.)
4. Lashley, K. S. The mechanism of vision: XVIII. Effects of destroying the visual "associative areas" of the monkey. *Genet. Psychol. Monogr.*, 1948, 37:107-166.

5. Mishkin, M. Visual discrimination performance following ablations of the temporal lobe: II. Ventral surfaces vs. hippocampus. *J. comp. physiol. Psychol.*, 1954, 47:187-193.
6. Mishkin, M. and Pribram, K. H. Visual discrimination performance following partial ablations of the temporal lobe: I. Ventral vs. lateral. *J. comp. physiol. Psychol.*, 1954, 47:14-20.
7. ———. Analysis of the effects of frontal lesions in monkey: II. Variations of delayed response. (Submitted for publication to *J. comp. physiol. Psychol.*)
8. Pribram, Helen and Barry, J. Further behavioral analysis of the parieto-temporo-preoccipital cortex. (Submitted to *J. Neurophysiol.*)
9. Pribram, K. H. and Bagshaw, M. H. Further analysis of the temporal lobe syndrome utilizing fronto-temporal ablations. *J. comp. Neurol.*, 1953, 99:347-375.
10. Pribram, K. H. and Fulton, J. F. An experimental critique of the effects of anterior cingulate ablations in monkey. *Brain*, 1954, 77:34-44.
11. Pribram, K. H. and Kruger, L. Functions of the olfactory brain. *Ann. N. Y. Acad. Sci.*, 1954, 58:109-138.
12. Pribram, K. H. and Mishkin, M. Analysis of the effects of frontal lesions in monkey: III. Object alternation. (Submitted for publication to *J. comp. physiol. Psychol.*)
13. ———. Simultaneous and successive visual discrimination by monkeys with inferotemporal lesions. *J. comp. physiol. Psychol.* (In press.)
14. Pribram, K. H., Mishkin, M., Rosvold, H. E., and Kaplan, S. J. Effects on delayed-response performance of lesions of dorsolateral and ventromedial frontal cortex of baboons. *J. comp. physiol. Psychol.*, 1952, 45:565-575.
15. Pribram, K. H. and Weiskrantz, L. The effect of selective resections of portions of the cerebral cortex on conditioned-avoidance performance of monkeys. (In preparation.)
16. Riopelle, A. J. and Ades, H. W. Discrimination learning following deep temporal lesions. *Amer. Psychologist*, 1951, 6:261 (Abstract).
17. Rose, J. E. and Woolsey, C. N. Organization of the mammalian thalamus and its relationships to the cerebral cortex. *EEG Clin. Neurophysiol.*, 1949, 1:391-404.
18. Rosvold, H. E., Mirsky, A. F., and Pribram, K. H. Influence of amygdalectomy on social interaction in a monkey group. *J. comp. physiol. Psychol.*, 1954, 47:173-178.

19. Wilson, W. and Mishkin, M. Survey of the effects of resection of the striate cortex and the infratemporal cortex on visually guided behavior. (In preparation.)

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