The intrinsic systems of the forebrain

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CHAPTER LIV

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CHAPTER CONTENTS

There remains yet another type of integration which claims consideration, although to saddle it upon nerve may perhaps encounter protest. Integration has been traced at work in two great, and in some respects counterpart, systems of the organism. The physico-chemical (or for short physical) produced a unified machine from what without it would be merely a collocation of commensal organs. The psychical, creates from psychical data a percipient, thinking and endeavouring mental individual. Though our exposition kept these two systems and their integrations apart, they are largely complemental and life brings them co-operatively together at innumerable points. . . . For our purpose the two schematic members of the puppet pair which our method segregated require to be integrated together. Not until that is done can we have before us an approximately complete creature of the type we are considering. This integration can be thought of as the last and final integration.

But theoretically it has to overcome a difficulty of no ordinary kind. It has to combine two incommensurables; it has to unite two disparate entities. To take an example: I see the sun; the eyes trained in a certain direction entrap a tiny packet of solar radiation covering certain wave-lengths emitted from the sun rather less than 10 minutes earlier. This radiation is condensed to a circular patch on the retina and generates a photo-chemical reaction, which in turn excites nerve-threads which relay their excitation to certain parts of the brain, eventually to areas in the brain-cortex. From the retina onward to the brain the medium of propagation is wholly nervous; that is to say, the reaction can be subsumed as electrical. Some of this electrical reaction generated in the eye does not reach the brain-cortex but diverges by a side-path into nerve-threads which relay it to a small muscle, which by contracting prevents excess of light attaining the retina. The electric current propagated to the muscle activates the muscle. The chain of events stretching from the sun's radiation entering the eye to, on the one hand, the contraction of the pupillary muscle, and on the other to the electrical disturbances in the brain-cortex are all straightforward steps in a sequence of physical 'causation', such as, thanks to science, are intelligible. But in the second serial chain there follows on, or attends, the stage of brain-cortex reaction an event or set of events quite inexplicable to us, which both as to themselves and as to the causal tie between them and what preceded them science does not help us; a set of events seemingly incommensurable with any of the events leading up to it. The self 'sees' the sun; it senses a two-dimensional disk of brightness, located in the 'sky', this last a field of lesser brightness, and overhead shaped as a rather flattened dome, coping the self, and a hundred other visual things as well. Of hint that this scene is within the head there is none. Vision is saturated with this strange property called 'projection', the unargued inference that what it sees is at a 'distance' from the seeing 'self'. Enough has been said to stress that in the sequence of events a step is reached where a physical situation in the brain leads to a psychical, which however contains no hint of the brain or any other bodily part. We cannot of course suppose that in the instance taken, the 'seeing the sun' breaks into a visual vacuum; in the waking day 'seeing' of some sort is always going on: on the physical side similarly electrical waves in the brain from one source or another must be practically unremitting during the waking day. The supposition has to be, it would seem, two continuous series of events, one physico-chemical, the other psychical, and at times interaction between them.

This is the body-mind relation; its difficulty lies in its 'how'. . . .

. . . Instead of, as is usual in physiology, leaving that impasse unmentioned, it seemed better to draw attention to it by the experimental observations in this book's final chapter.

SHERRINGTON, C. S. *The Integrative Action of the Nervous System.* Foreword to 1947 Edition (129).

INTRODUCTION

FOR THE PAST CENTURY and a half, the 'mind-body' problem has been focused on the relationship between the functions of the cerebral mantle and mental processes. The question is often raised as to whether mental processes—especially 'complex' mental processes such as ideas, attitudes and thoughts—are radically (incommensurably) different from the physiological and the physical. With regard to elementary sensory and motor events (such as depressing a key when a light is flashed), the scientist proceeds upon the basis that psychological concepts (here the visual field) are inferred from observations and measurements of organism-environment interactions, interactions that can be specified by the use of physiological, physical and behavioral methods. Experimental evidence is presented here that more complex mental processes—such as thought, attitude, value—can also be studied in this manner: that environmental, organismic and behavioral referents for these processes can be specified--that, therefore, the difference between the psychological processes designated as complex and those designated as elementary is not a radical one.

Complex mental processes are most readily inferred from observations of problem-solving behavior. Those portions of the cerebral mantle devoid of any major direct connections with peripheral structures have been consistently linked with problem-solving processes and have, therefore, been of especial interest to students of the mind-body relationship. The designation 'association cortex' has obscured a considerable ignorance concerning the functions of these parts of the brain. The designation was framed within the empiricist tradition as this had evolved up to the latter part of the past century, and presupposes anatomical and physiological evidence for the notion of a transcortical reflex. Data are presented here upon which an alternative conception is proposed.

Definition of Intrinsic Systems of the Forebrain

The conception of an 'association cortex' stems from the fact that certain parts of the forebrain have obvious major direct connections with peripheral structures while others do not. This difference has been used by Rose & Woolsey (124) in a rigorous classification of the subdivisions of the dorsal thalamus – the forebrain structure which, as a whole, serves as the final discontinuity intercalated between peripherally initiated neural events and those of the endbrain. These investigators suggest the term 'intrinsic' for those portions of the dorsal thalamus in which no major extrathalamic, extratelencephalic afferents terminate. The intrinsic portions of the thalamus project to those sectors of the cerebral mantle usually referred to as 'association cortex.' As already noted, the term 'association cortex' has its disadvantages: 'association' makes the unsupported assumption that in these areas, convergent tracts bring together 'sensory' events transmitted from the 'receiving areas' of the brain. Throughout this presentation, therefore, the currently less loaded term 'intrinsic sectors' will be substituted for 'association cortex'; 'intrinsic systems' will be used when reference is made to the thalamic projection as well as to the related cortical area.

The key to an analysis of the functions of the intrinsic systems of the forebrain is obtained from a study of the organization of the mammalian thalamus. On the basis that some of the nuclear groups within the thalamus bear a fairly consistent relation to one another, an external portion and an internal core of the thalamus can be distinguished (59). The external portion is composed of the ventral, the posterior (lateral and pulvinar) and the geniculate nuclei (fig. 1). In carnivores and primates this external portion is, for a considerable extent, demarcated from the internal core of the dorsal thalamus by an aggregation of fibers, the internal medullary lamina and its rostral extensions surrounding the anterior nuclear group. The internal core of the dorsal thalamus may also be subdivided into three large groups: the anterior, the medial and the central (mid-line and intralaminar) nuclei.

Each of the major subdivisions (external and internal) may be further characterized according to the type of its nontelencephalic major afferents (fig. 2). Thus, the ventral and geniculate nuclei of the external division are the terminations of the large topologically discrete 'specific' afferent tracts (e.g. spinothalamic, trigeminal, lemniscal and the brachium conjunctivum, as well as the otic and optic radiations) of the somatic, gustatory, auditory and visual systems (144). Within the internal core, the anterior nuclei receive an input from the posterior hypothalamus through the mammillothalamic tract; the central nuclei receive nonspecific diffuse afferents by way of the reticular forma-

Electrophysiology (e.g. Magoun, 1950; Starzl, et al., 1951) Silver stain (Morin, et al., 1951)	Comparative histomorphology (e.g. Koppers, Huber & Crosby, 1936; Rose & Woolsey, 1949)	Retrograde thalamic degeneration after cortical removals, Monkey. (e.g. Walker, 1938; Chow, 1950; Chow & Pribram, 1956; Pribram et al., 1953)	Cytoarchitecture & Strychnine neuronography (e.g. v. Bonin & Bailey, 1947; Bailey, v. Bonin & McCulloch, 1950; MacLean & Pribram, 1953; Pribram & MacLean, 1953)

External Portion

*Posterior
- n. lateralis posterior ———— Posterior parietal cortex
- n. pulvinaris ———— Posterior parietal & temporal cortex & anterior occipital cortex

Eugranular isocortex of the parietal, temporal & occipital lobes (the posterior "association" cortex)

Ventral
- n. ventralis anterior ———— Dorsal frontal cortex
- n. ventralis lateralis ———— Precentral cortex
- n. ventralis posterior (basalis) ———— Rolandic cortex

Mode-Specific Discrete Input

Geniculate
- n. geniculatus medialis ———— Posterior supratemporal plane & posterior insular cortex
- n. geniculatus lateralis ———— Striate occipital cortex

Agranular, dysgranular & konioisocortex

Internal Core

Anterior
- n. anterior dorsalis ———— Retrosplenial cingulate cortex
- n. anterior ventralis ———— Posterior cingulate cortex
- n. anterior medialis ———— Anterior cingulate cortex

Non-Specific Diffuse Input

Central
- nuclei of the midline (e.g. n. reuniens) ———— Subcallosal & medial orbital cortex
- intralaminar nuclei (e.g. n. centralis medialis) ———— Orbitofronto-insulo-temporal cortex & basal ganglia (caudate)
- n. centromedianum ———— Basal ganglia (putamen)

Allo- & juxtallocortex of the limbic portions of the hemispheres & closely related subcortical forebrain structures

*Medial
- n. medialis dorsalis ———— Anterofrontal cortex

Frontal eugranular isocortex (the frontal "association" cortex)
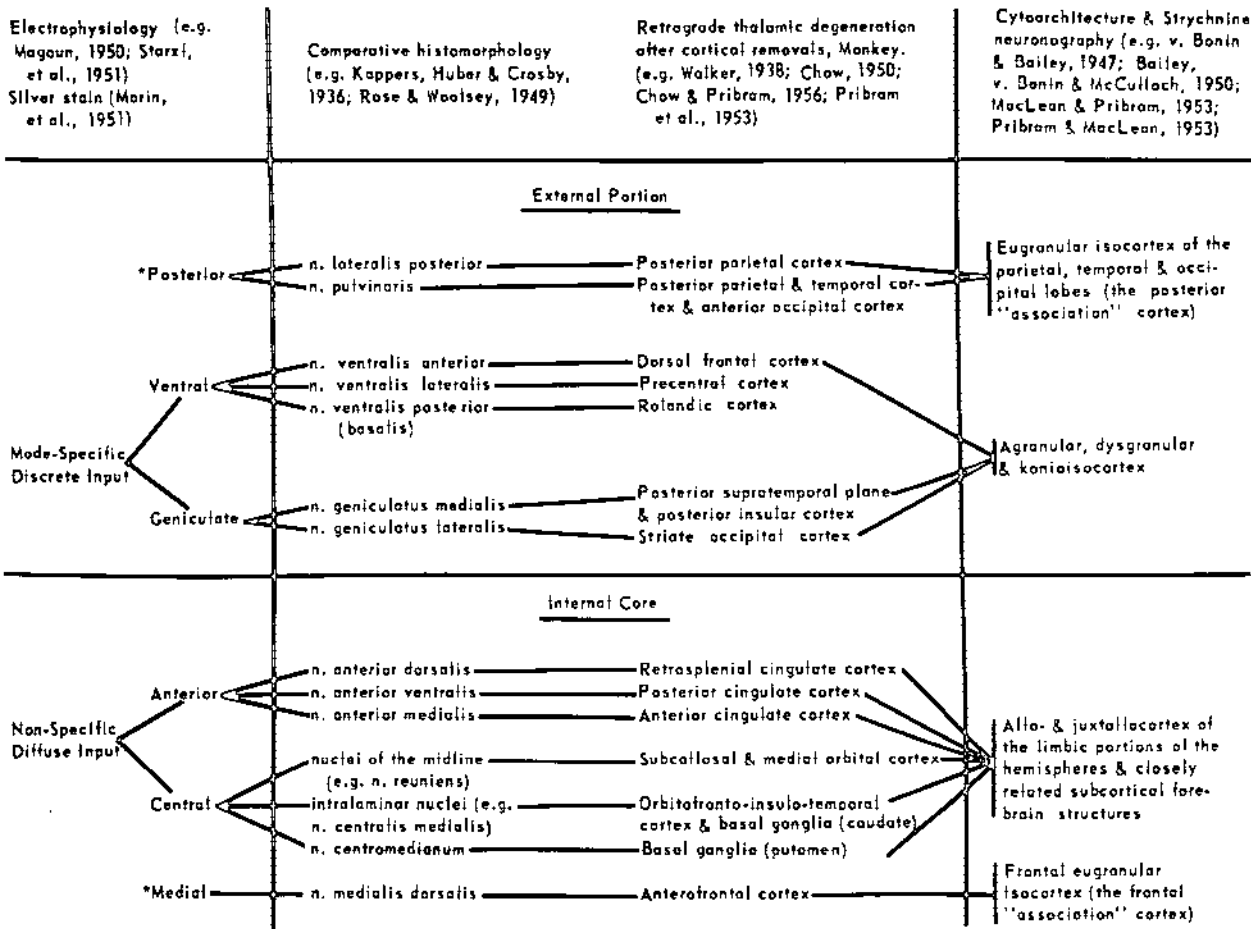
FIG. 1. Diagram of the distinctions between an internal core and an external portion of the forebrain. Examples of the techniques and particular studies invoked in making the classification are given in the *upper column*. As in any such classification, its heuristic value should not obscure its deficiencies. There is, of course, a multiplicity of forebrain systems, each of which partakes to a greater or less extent of the characteristics defining the internal core and those defining the external portion. In general, however, the nearer a system is to the central canal (or ventricular system) of the central nervous system, the greater the number of its 'internal core' characteristics; the further from the central canal, the greater the number of its 'external portion' characteristics. Also, the interaction of these various systems must not be ignored; this scheme is a restricted analysis and does not deal with such interactions.

tion of the mesencephalon and, in addition, a probable input from the anteromedial hypothalamus (95, 96).[1] Thus the constancies of morphology in the mammalian thalamus reflect certain gross distinctions which can be made in the types of afferents to the forebrain.
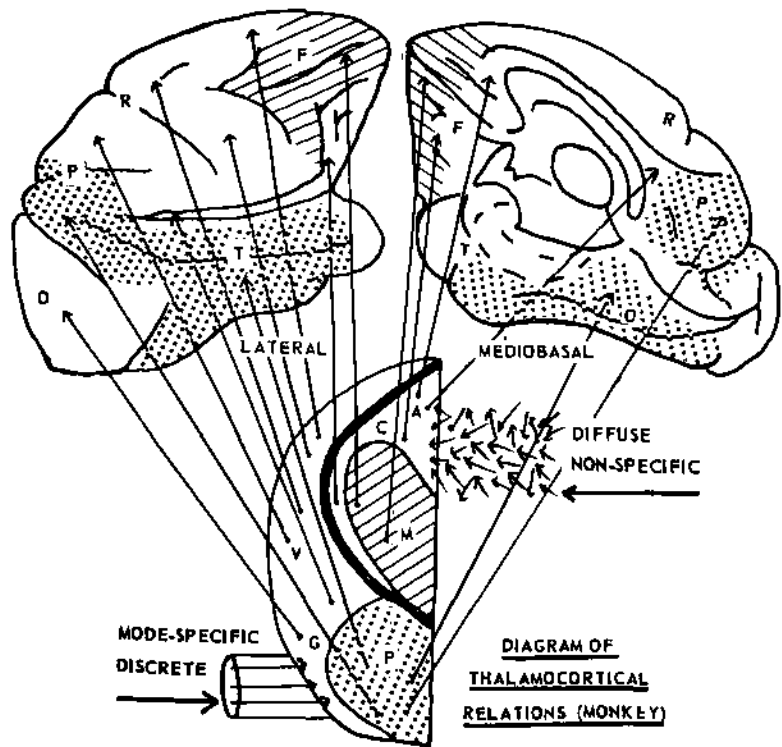
The other two nuclear groups, the posterior in the

[1] In this respect, the classification presented here differs from that of Rose and Woolsey. These authors do not accept the evidence from silver-stained preparations as indicating a major extrathalamic, extratelencephalic input. Heuristically, such evidence is accepted here.

external portion and the medial in the internal core, do not receive any such major extrathalamic afferents and, as noted above, are therefore classified as the 'intrinsic' nuclei of the thalamus (124). Important to the argument presented here is the fact that an intrinsic nucleus is assigned to each of the major thalamic divisions (see fig. 2).

The telencephalic projections of the external portion of the dorsal thalamus terminate in the dorsolateral and posterior cortex (figs. 1, 2). The termination of the telencephalic projections of the internal core is in the frontal and mediobasal portions of the

FIG. 2. Schematic representation of the projections from the dorsal thalamus to the cerebral cortex in the monkey. The *lower half* of the figure diagrams the thalamus, the *straight edge* representing the mid-line; the *upper half* of the figure shows a lateral and mediobasal view of the cerebral hemispheres. The *broad black band* in the thalamic diagram indicates the division between an internal core which receives a nonspecific diffuse input and an external portion which receives the modality-specific discrete projection tracts. The *stippled* and *crosshatched* portions represent the intrinsic systems: the medial nucleus of the internal core and its projections to the anterofrontal cortex; the posterior nuclear group of the external portion of the thalamus and its projections to the parietotemporooccipital cortex. The boundaries of the cortical sectors of the intrinsic systems are not sharp and as yet not precisely defined—thus, this diagram is to be read as a tentative approximation, based on currently available evidence. *F*, frontal; *R*, rolandic; *P*, parietal; *T*, temporal; *O*, occipital; *A*, anterior; *C*, central; *M*, medial; *V*, ventral; *G*, geniculate; *P*, posterior.

forebrain and includes the basal ganglia. Specifically, the ventral group of the external portion of the dorsal thalamus projects to the dorsolateral cortex of the frontal and parietal lobes (15, 144); the geniculate groups, to the lateral portion of the temporal and the posterior portion of the occipital lobe (144); the posterior nuclear group, to the remaining cortex of the parietotemporoprecoccipital (P.T.O.) convexity (10, 15).

Within the internal core (figs. 1, 2), the medial nuclei project to the anterofrontal cortex (or orbito-frontal, as it has been called in subprimate mammals) (86, 112, 123, 144). The anterior and the central nuclei project to the medial and basal forebrain structures, the anterior nuclei to the cingulate areas on the medial surface of the frontal and parietal lobes (73, 86, 106, 113, 122, 125, 146); the central nuclei project (5, 20, 98, 105, 111, 124) to the anterior rhinencephalic and closely related juxtallocortical areas and basal ganglia [the second rhinencephalic system as defined by Pribram & Kruger (114)].

In summary, an intrinsic nuclear group and its projections is described for each of the major thalamic subdivisions: a posterior intrinsic system, related to the external portion of the thalamus and the dorsolateroposterior cerebral convexity; a frontal intrinsic system, related to the internal core of the thalamus and the frontomediobasal areas of the cerebral hemispheres.

NEUROBEHAVIORAL ANALYSIS OF POSTERIOR INTRINSIC SYSTEM

As already noted, the forebrain may conveniently be divided into two major portions, a dorsolatero-posterior and an anteromediobasal. In primates each of these major portions contains intrinsic sectors: posterior intrinsic sectors (the classical sensory association areas) (108), and a frontal intrinsic sector (the classical frontal association area) (110). Neurobehavioral experiments performed during the past 25 years have shown these intrinsic sectors to be especially related to problem-solving processes (51, 107). The aim of this, and of the following sections, is to specify in detail this relationship.

An Experiment

A modified Wisconsin General Testing Apparatus (49) is used to test 12 rhesus monkeys in the solution of a complex problem. The monkeys are divided into three groups, two operated and one control, each containing four animals. The animals in one operated

group had undergone bilateral cortical resections in the posterior intrinsic cortex, and those in the other operated group bilateral cortical resections in the frontal intrinsic cortex some $2\frac{1}{2}$ years prior to the onset of the experiment (fig. 3); those in the control group are unoperated. In the testing situation these animals are confronted initially with two junk objects placed over two holes (on a board containing 12 holes in all) with a peanut under one of the objects. An opaque screen is lowered between the monkey and the objects as soon as the monkey has displaced one of the objects from its hole (a trial). When the screen is lowered, separating the monkey from the 12-hole board, the objects are moved (according to a random number table) to two different holes on the board. The screen is then raised and the animal is again confronted with the problem. The peanut remains under the same object until the animal finds the peanut five consecutive times (criterion). After a monkey reaches criterion performance, the peanut is shifted to the second object and testing continues (discrimination reversal). After an animal again reaches criterion performance a third object is added (fig. 4). Each of the three objects in turn becomes the positive cue; testing then proceeds as before—the screen separates the animal from the 12-hole board, the objects are placed randomly over three out of the 12 holes (with a peanut concealed under one of the objects), the screen is raised, the animal is allowed to pick an object (one response per trial), the screen is lowered and the objects are moved to different holes. The testing continues in this fashion until the animal reaches criterion performance with each of the objects positive in turn. Then a fourth object is added and the entire procedure repeated. As the animal progresses, the number of objects is increased serially through a total of 12 (fig. 5). The testing procedure is the same for all animals throughout the experiment; however, the order of the introduction of objects is balanced—the order being the same for only one monkey in each group.

Analysis of the problem posed by this experiment indicates that solution is facilitated when a monkey attains two strategies: a) during search– moving, on successive trials, each of the objects until the peanut is found; b) after search—selecting on successive trials the object under which the peanut had been found on the preceding trial. During a portion of the experiment, searching is restricted in animals with posterior intrinsic sector ablations, and selection of the object under which the peanut had been found on the previous trial is impaired by frontal intrinsic sector
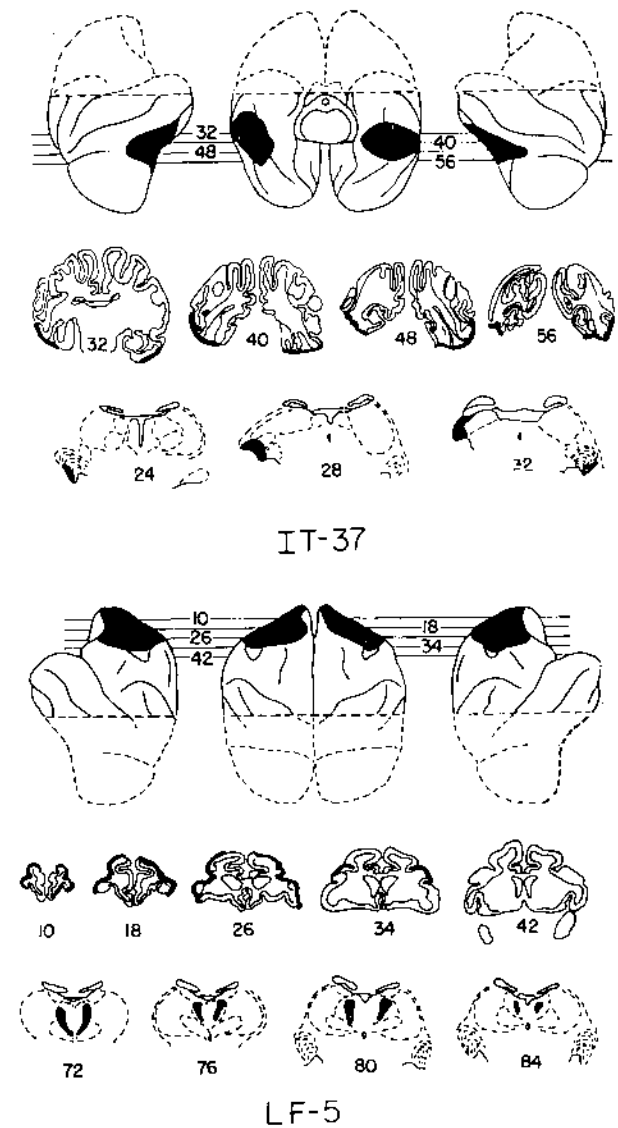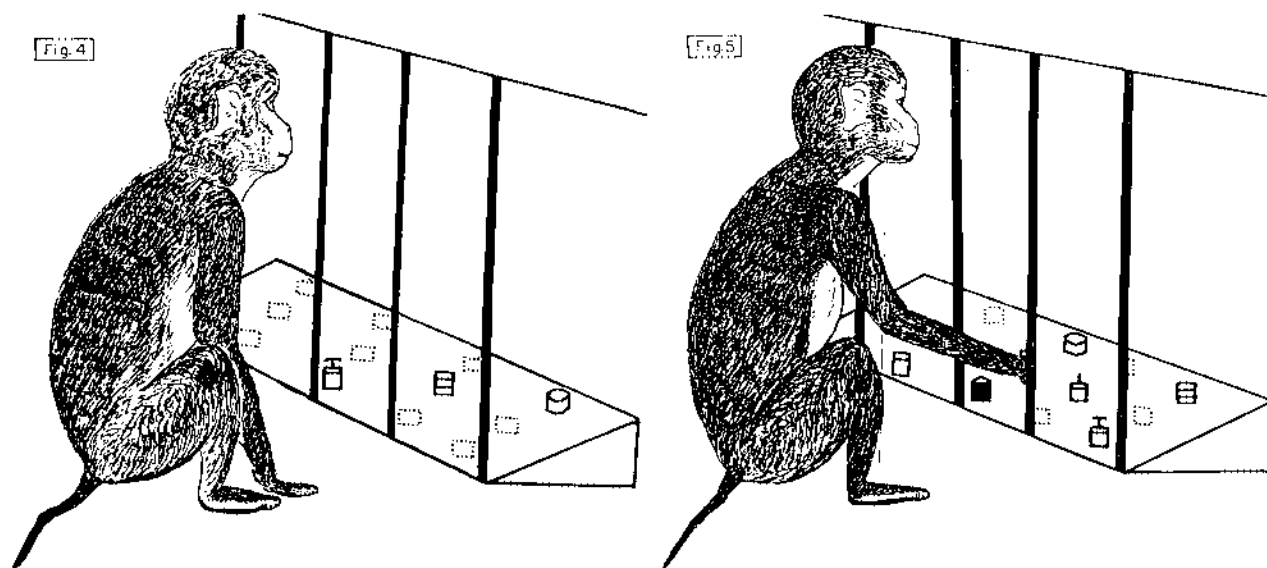

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FIG. 3. Representative reconstructions and cross sections through the cortex and thalamus showing extent of the lesions in the posterior (*upper figure*) and frontal (*lower figure*) intrinsic systems. Cortical lesion and resulting thalamic degeneration shown in *black*.

ablations. The effects of the posterior intrinsic sector lesion will be dealt with first.

Figure 6 graphs the averages of the total number of repetitive errors made by each of the groups in each situation. Comparison of figure 6 with figure 7, representing the repetitive errors made by each group in each situation during search, illustrates that the deficit of the frontally operated group is not associated with search (a result that is discussed below); however, the peak and general shape of the error curves

FIGS. 4 AND 5. Diagrams of the multiple object problem showing examples of the three and the seven object situations. Food wells are indicated by *dashed circles*, each of which is assigned a number. The placement of each object over a food well was shifted from trial to trial according to a random number table. A record was kept of the object moved by the monkey on each trial, only one move being allowed per trial. Trials were separated by lowering an opaque screen to hide from the monkey the objects as they were repositioned.

describing the performance of the control and posteriorly operated groups are similar whether total repetitive errors (fig. 4) or search errors (fig. 7) are plotted. In spite of the increasing complexity of the succeeding situation, the curves appear little different from those previously reported to describe the formation of a discrimination in complex situations (8, 130). Although one might a priori expect the number of repetitive responses to increase monotonically as a function of the number of objects in the situation, this does not happen. Rather, during one or another phase of the discrimination, the number of such responses increases to a peak and then declines to some asymptotic level (8, 130). Analysis of the data of the present experiment has shown that these peaks or 'humps' can be attributed to the performance of the control and posteriorly operated groups during the initial trials given in any particular (e.g. 2, 3, 4 ⋯ cue) situation —i.e. when the monkey encounters a novel object. The period during which the novel and familiar objects are confused is reflected in the 'hump' (fig. 8). The importance of experience as a determinant of the discriminability of objects has been emphasized by Lawrence (75, 76). His formulation of the 'acquired distinctiveness' of cues is applicable here. In a progressively more complex situation, sufficient familiarity with all of the objects must be acquired before a novel

object is sufficiently distinctive to be readily discriminated.

But there is a difference between the control and the posteriorly operated groups as to when the confusion between novel and familiar objects occurs. The peak in errors for the group with posterior lesions lags behind that for the controls—a result which forced attention because of the paradoxically 'better performance' of this group throughout the five- and six-cue situations (in an experiment which was originally undertaken to demonstrate a relation between number of objects in the situation and the discrimination 'deficit' previously shown by this group).

These paradoxical results are accounted for by a formal treatment based on mathematical learning theory: on successive trials the monkeys had to 'learn' which of the objects now covered the peanut and which objects did not. At the same time they had to 'unlearn,' i.e. extinguish, what they had previously learned— under which object the peanut had been and under which objects it had not been. Both neural and formal models have been invoked to explain the results obtained in such complex discrimination situations. Skinner (130) postulated a process of neural induction to account for the peak in errors—much as Sherrington had postulated 'successive spinal induction' to account for the augmentation of a crossed extension
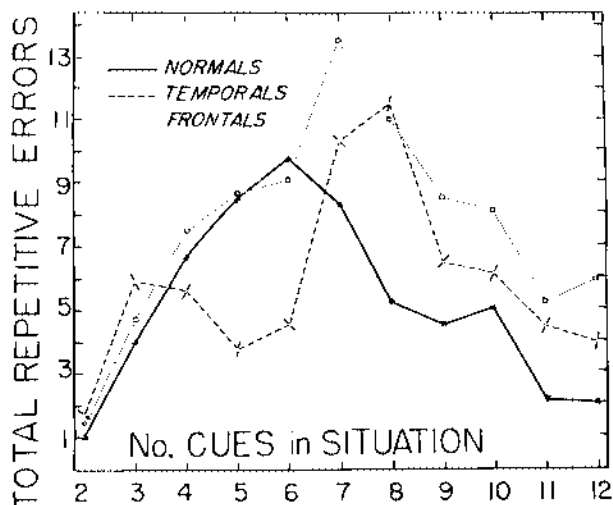
FIG. 6. Graph showing the average of the total number of repetitive errors made in each of the situations in the multiple object experiment by each of the groups: control animals (*Normals*); animals with posterior intrinsic sector lesions (*Temporals*); and animals with frontal intrinsic sector lesions (*Frontals*). A situation is defined by the number of objects in the problem and includes successions of trials. During each succession the peanut is consistently placed under one of the objects (cues). The succession is terminated when the monkey has moved the object under which the peanut is placed on five consecutive trials (criterion). (See also the legends to figs. 4, 5 and 10.) A repetitive error is made by a monkey when during a succession of trials he moves more than once an object other than the one under which the peanut is placed.
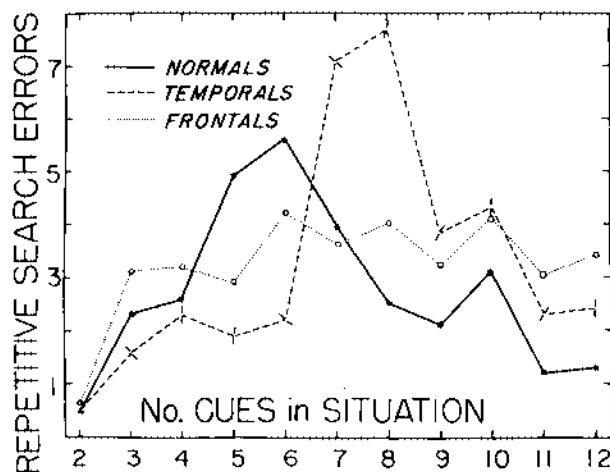
FIG. 7. Graph of the average of the number of repetitive errors made in the multiple object experiment by each of the groups during search (see legend to fig. 6). Search trials are those anteceding the first 'correct' response in a succession of trials, i.e. those anteceding the movement of the object (cue) under which a peanut has been placed. Note the difference between the location of the 'hump' in the graph of the normal controls and in that of the group with posterior lesions (*Temporals*).

reflex by precurrent antagonistic reflexes (such as the flexion reflex). Several of Skinner's pupils (24, 46a) have developed formal models. These models are based on the idea that both 'learning' (or 'conditioning') and 'unlearning' (or 'extinction') involve antagonistic response classes—that in both conditioning and extinction there occurs a transfer of response probabilities between response classes. This conception is, of course, similar to Sherrington's description of the interaction of antagonistic reflexes: "... *this* reflex or *that* reflex but not the two together." The resulting equations that constitute the model contain a constant which is defined as the probability of sampling a particular stimulus element (46a), namely the object, in the discrimination experiment presented here. This constant is further defined (Estes) as the ratio between the number of stimulus elements sampled and the total number of such elements that could possibly be sampled. This definition of the constant postulates that it is dependent for its determination upon both environmental and organismic factors. According to the model the rapidity of in-

crease in errors in a discrimination series depends on this sampling ratio—the fewer objects sampled, the more delayed the peak in recorded errors. The paradox that for a portion of the experiment the group with posterior lesions performs better than the control group stems from the relative delay in the peak of the recorded errors of the operated group.[2] The model

[2] The actual model used to interpret the data analyzed here was developed by Green (46a) and is patterned after a model of discrimination learning proposed by Bush & Mostellar (8). The Green model takes its roots from a parallel model originated by Estes (24, 25). The general form of the model is derived from Estes' equations describing the conditioning and extinction processes:

$\bar{p}_n(S - I) + 1 - (1 - \bar{p}_0)(1 - \theta_1)^{xn}$ for conditioning to those elements which constitute occasions for reinforcement,

$\bar{p}_n(S' - I) + \bar{p}_0(1 - \theta_2)^{xn}$ for extinction to those elements which are never occasions for reinoforcement, and

$$\bar{p}_n(I) = \frac{\pi\theta_1}{\pi\theta_1 + \pi\theta_2} - \left[\frac{\pi\theta_1}{\pi\theta_1 + \pi\theta_2} - \bar{p}_0\right](1 - \pi\theta_1 - \pi\theta_2)^n$$

for the changes associated with intercept elements, i.e. those present on both reinforced and unreinforced occasions;

where

S represents the stimulus elements (objects) which are reinforced (have peanuts under them),

FIG. 8. Graph of the average of the number of repetitive errors made in the multiple object experiment during those search trials in each situation when the additional, i.e. the novel, cue is first added. Note that the peaks in errors shown in fig. 7 are accounted for by the monkey's confusion between novel and familiar objects as graphed here.
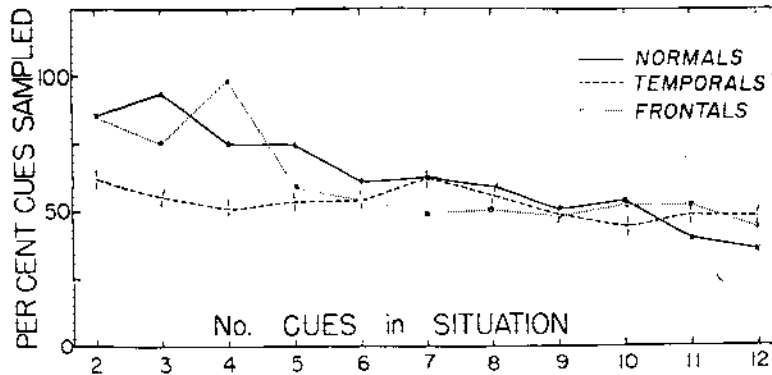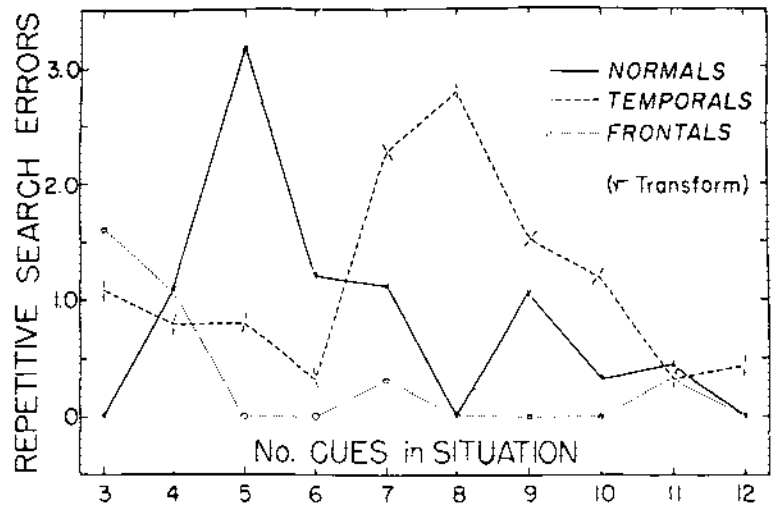

FIG. 9. Graph of the average of the per cent of the total number of objects (cues) that are sampled by each of the groups in each of the situations (see legend to fig. 6). To sample, a monkey had to move an object until the content or lack of content of the food well was clearly visible to the experimenter. As was predicted (see text), during the first half of the experiment the curve representing the sampling ratio of the posteriorly lesioned group differs significantly from the others at the .024 level [according to the nonparametric Mann-Whitney U procedure (84)].

predicts, therefore, that this operated group has sampled fewer objects during the early portions of the experiment. This prediction is tested as shown in the graph of figure 9.

The prediction is confirmed. The posterior intrinsic sector is thus established as one of the organismic variables that determine the constant of the model. As postulated by the model, the ratio of objects sampled

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S' represents those stimulus elements which are not reinforced,

I represents the overlap between S and S' which expresses confusion when reinforcement is shifted from one to another object,

π represents the relative frequency of reinforced trials in the stimulus series,

$\bar{\pi}$ represents the relative frequency of nonreinforced trials in the stimulus series,

$\bar{p}_n$ represents the mean probability of response on the nth trial,

$\bar{p}_0$ represents the initial probability of response (operant level),

θ_1 and θ_2 represent the sampling ratios for reinforced and nonreinforced stimulus sets respectively, and

n denotes the number of trials.

It is assumed that the above equations are weighted directly as a function of the proportion of elements within the intercept and nonintercept subsets, such that

$$\bar{p}_n(S') = k'\bar{p}_n(S' - I) - (1 - k')\bar{p}_n(I)$$

In these experiments, then,

S' is the set of unreinforced stimulus elements (objects under which no peanut is located),

I includes among the subset of elements common to both reinforced and unreinforced trials those objects which 'recently' have had a peanut under them,

k' is the proportion of stimulus elements not common to both reinforced and unreinforced trials, and

$\bar{p}_n(S')$ is the mean probability of response on nonreinforced trials (probability of error responses) on the nth trial.

In the present experiment only the objects with no peanuts under them are considered since only one object at a time had a peanut under it. Thus the set of reinforced objects reduces to one, and the sampling ratio associated with it θ_1 is maximized with respect to the sampling ratio associated with the unreinforced sets, θ_2.

turns out to be more basic than the number of objects in the situation per se.

Review of Other Data

The lag in attaining the strategy to sample extensively shown by monkeys with posterior intrinsic sector lesions is correlated with other deficiencies in differentiation that follow such lesions. These deficiencies differ in some respects from those produced by lesions of the extrinsic (classical 'primary projection') systems, but the differences are subtle and have repeatedly eluded precise specification (116). The available data may therefore be briefly reviewed in a renewed attempt at such specification. *a*) Drastic bilateral removal of an extrinsic sector severely limits differentiative behavior in the modality and only in the modality served by that sector. The limitation affects practically all differentiations in the mode: thus, a monkey in which the occipital lobes have been removed reacts only to gross changes in the environment that affect the visual receptors—changes that can be ascribed to variations in total luminous flux (61). Comparably, drastic bilateral removal of a posterior intrinsic sector restricts differentiative behavior within the mode served by that sector, and only within that mode, but the limitation is not as severe as that produced by drastic removal of the extrinsic sector serving that mode (14, 107). *b*) Under some conditions, differentiation is unimpaired after drastic posterior intrinsic sector resection: for example, after such a removal, a monkey can catch a flying gnat in mid-air and can pull in a peanut which is beyond reach but attached to an available fine silk thread (0000 surgical). In these situations, as in situations that necessitate the opening of a single box or depressing of a single lever, the operated animal is indistinguishable from an unoperated control (108). *c*) Under other conditions, such as those in the experiment described above, differentiation is impaired after posterior intrinsic sector ablations. These conditions have in common the requirement that two or more separate responses be systematically related to the differences between the environmental events that determine the stimulus; i.e. alternatives are available to the organism, alternatives that are specified by environmentally determined stimuli. Such stimuli, for convenience, will hereafter be referred to as 'input' variables. Examples of the problems where impairment is found in the visual mode are: brightness, color, form, pattern, size and flicker discriminations (90–92); successive and simultaneous discriminations (116);

successions of discriminations ('learning set') (12, 120); oddity discriminations (50); and matching from sample (50). Although the operated animals may perform 'normally' on particular problems within a problem group, decrement is found on other more 'difficult' problems in that group. Difficulty of problem is independently defined by the number of trials taken by naive unoperated animals to learn the problem. In most instances problem difficulty has also been related to differences between the physical dimensions of the objects, such as size discrimination (91), and to other determinants of the alternatives in the situation, including situational differences (116) and sampling in the multiple-object problem.

Analysis of Results

These then are the data. Extensive bilateral ablations of both extrinsic and posterior intrinsic sectors impair differentiative behavior, but differences between the impairments exist. Attempts to portray these differences are familiar. Neurologists have spoken of 'defective sensibility' and of 'agnosia' (33, 52), the latter often conceived as a disorder of memory. In so far as this distinction assumes an associationistic model of the functions of the intrinsic sectors, it gains little support from neurological or neuropsychological evidence (108). An alternate view can be proposed. Psychologists have spoken of 'existential discriminations' and 'differential discriminations' (57), or of 'sensibility' and 'intelligibility' (89), distinctions that are made on the basis of whether the organism's actions are determined by 'simple presence or absence' of input variables or by 'some more complex relationship' between these variables, such as the number of 'contextual alternatives' in the situation (88). The results of the experiment reported in this presentation warrant an attempt to pursue this conceptualization of the distinction by proposing a formal model of the interaction between the functions of the intrinsic and extrinsic sectors in differentiative behavior.

The defect in differentiative behavior that results from lesions of the extrinsic and posteror intrinsic sectors of the forebrain can be characterized by stating the variety of transformations of the input under which behavior remains invariant. Following extensive bilateral resections of the extrinsic sectors, behavior remains invariant under a great variety of transformations of the input. For instance, for these preparations, even brightness and size of luminant are multiplicatively interchangeable quantities (61), whereas differentiative behavior by organisms with

intact extrinsic sectors is invariant under much more restricted ranges of transformations of the input -such as differentiation in the case of contrast and contour (80), texture and acuity (39); continuous (orthogonal) projective in the case of position, distance, form and rigid motion (40, 41, 43).

The effects of lesions of the posterior intrinsic sectors can also be characterized usefully in this way. Differentiative behavior which remains invariant under still fewer transformations of the input is interfered with by such lesions. In the extreme, unique responses, i.e. 'absolute' differentiations, would be most affected.

Unique responses can occur only when both an 'absolute' unit and an 'absolute' reference point have been fixed. As indicated in the discussion of the results of the multiple object experiment, the mathematical learning theory provides an approach to the specification of these units and their referents. The fact that this mathematical device has proved so powerful a tool in the analysis of some completely unexpected effects of posterior intrinsic sector lesions lends support to its usefulness in the development of the model.

MODEL OF POSTERIOR INTRINSIC MECHANISM

Deficiencies of Transcortical Reflex

Models of cerebral organization relevant to complex psychological processes have been based to a large extent on clinical neurological data and have been formulated with the 'reflex' as prototype. Such models, implicitly or explicitly, assume that the effects of receptor activity are transmitted to receiving or sensory areas; from these, neural activity converges upon the association cortex where 'elaboration' takes place; the 'elaborated' or 'associated' neural events are then relayed to the 'motor' cortex which is considered the final common path for all cerebral activity. These models fail to take into account the finding that extratelencephalic afferents reach the portions of the cortex usually referred to as 'motor' as well as those known to be 'sensory.' Nor do they consider the extent of the origin of efferents from the cerebral mantle, an extent which includes the 'receiving' as well as the 'motor' areas.

Electrophysiological and neuroanatomical experiments demonstrate that somatic afferents are distributed to both sides of the central fissure of primates (1, 38, 66, 82, 126, 152). A recent monograph (74) documents thoroughly the evidence for a more ex-

tensive origin of the pyramidal tract from the entire extent of the postcentral as well as from the precentral cortex of primates. This marked afferent-efferent overlap is not limited to the somatic system. With respect to vision, eye movements can be elicited from stimulation of practically all of the striate cortex (145); these eye movements can be elicited after ablation of the other cortical areas from which eye movements are obtained. With respect to audition, ear movements have been elicited from the auditory system (137). From the portion of the cortex implicated in gustation, tongue and chewing movements may be elicited (5, 136); respiratory effects follow stimulation of the olfactory 'receiving' areas (58, 114). Thus, an overlap of afferents and efferents is evident not only in the neural mechanisms related to somatic function but also in those related to the special senses. The overgeneralization to the brain of the law of Bell and Magendie (81) which defines 'sensory' in terms of afferents in the dorsal spinal and 'motor' in terms of efferents in the ventral spinal roots must, therefore, give way to more precise investigation of the differences in internal organization of the afferent-efferent relationship between periphery and cortex in order to explain differences such as those between 'sensory' and 'motor' mechanisms. As yet, only a few experiments toward this end have been undertaken (4, 16, 121).

The afferent-efferent overlap in these projections, or to use a term that takes account of this afferent-efferent overlap, these 'extrinsic' systems, suggests the possibility that the intrinsic systems need not be considered as association centers upon which pathways from the sensory sectors converge to bring together neural events before these can determine movement via the motor pathways. A series of neurobehavioral studies (11, 26, 70, 131, 132, 143), in which the extrinsic sectors were surgically crosshatched, circumsected or isolated by large resections of their surround with little apparent effects on behavior, has cast further doubt on the usefulness of a 'transcortical' reflex model. Additional difficulties are posed by the negative electrophysiological and anatomical findings whenever direct connections are sought between the extrinsic and intrinsic sectors (115, 138). Experimentalists who followed Flourens in dealing with this problem, including Munk (97), von Monakov (139), Goldstein (45), Loeb (79) and Lashley (68), have invariably come to emphasize the importance of the extrinsic sectors not only in 'sensory-motor' behavior but also in the more complex psychological processes. Each investigator has had a slightly different approach

to the functions of the intrinsic sectors, but the viewpoints share the proposition that the intrinsic sectors do not function independently of the extrinsic. The common difficulty has been the conceptualization of this interdependence between intrinsic and extrinsic systems in terms other than the transcortical 'reflex' model—a model which became less cogent with each new experiment.

Partitioning of Sets

There is an alternative concept which meets the objections levied against the transcortical 'reflex' yet accounts for currently available data. The relationship between intrinsic and extrinsic systems can be attributed to convergence of efferents from the two systems at a subcortical locus, rather than to specific afferents from the extrinsic to the intrinsic cortex. Some evidence supporting this notion is already available. Data obtained by Whitlock & Nauta (150), using silver staining techniques, show that both the intrinsic and the extrinsic sectors implicated in vision by neuropsychological experiments are efferently connected with the superior colliculus. On the other hand, lesions of the intrinsic thalamic nuclei fail to interfere with differentiative behavior (13, 102). Thus, the specific effects in behavior of the intrinsic systems are explained on the basis of efferents to a subcortically located neural mechanism that has specific functions. These efferents can be conceived to partition the afferent activity that results in the events in the extrinsic sectors, events initiated by and corresponding to the input variables. Partitioning determines the extent of the range of possibilities to which an element or a set of elements can be assigned. Partitioning results in patterns of information, information given by the elements of the subsets resulting from the partition (140). The posterior intrinsic sector mechanism is thus conceived to provide both referent and units, though not the elements to be specified. The effect of continued intrinsic sector activity will, according to this model, result in a sequence of patterns of information (partitions) of increasing complexity, which in turn allow more and more precise specification of particular elements in the set (or subsets) of events occurring in the extrinsic systems. Thus, through continued posterior intrinsic sector activity, more and more information can be conveyed by any given input. As a result, the organism's differentiative behavior remains invariant under a progressively narrower range of systems of transformation of the input—differentiations become more 'absolute.'

The programing of the activities of the posterior intrinsic sectors remains in question. Some things are clear, however. The advantage of this model is that the program is not composed by the events upon which the program operates. In this respect the model is in accord with neural and neurobehavioral facts (108). Other models, whether associationistic or match-mismatch (6), demand the storage of an ever increasing number of 'bits' of information. The evidence is overwhelmingly against the presence in the nervous system of such minutely specific engrams (71). In the model here presented, engrams consist of encoded programs. These operate on the neural events that are initiated by the input, transforming them into other neural events which can lead to an ever increasingly finer, that is, a more appropriate, differential response (42, 148). In this formulation the posterior intrinsic sectors are conceived as programing mechanisms that function to partition events initiated by the input, not as the loci of association of such events, nor as the loci of storage of an ever increasing number of minutely specific engrams.

NEUROBEHAVIORAL ANALYSIS OF FRONTAL INTRINSIC SYSTEM

The mechanism by which the posterior intrinsic sectors is conceived to affect differential behavior finds a parallel in the mechanism by which the frontal intrinsic sector can affect intentional behavior. The demonstration of this parallel is most effectively initiated by some definitions that allow further analyses of the data obtained in the multiple object discrimination experiment.

Some Definitions

Behavior theory often begins with the statement that a response is a function of certain organismic variables (such as drive or habit) and of a 'stimulus' which is conceived as some environmental event or constellation of environmental events. This classical behaviorist position has been challenged by those primarily interested in psychophysical and perceptual problems (3, 135); these investigators are concerned with the more precise specification of the category 'stimulus' as including 'distal' (e.g. environmental) and 'proximal' (organismic, i.e. receptor) events. This concern must be shared by the neuropsychologist who is interested in the relationship between central processes and behavior since complex interactions
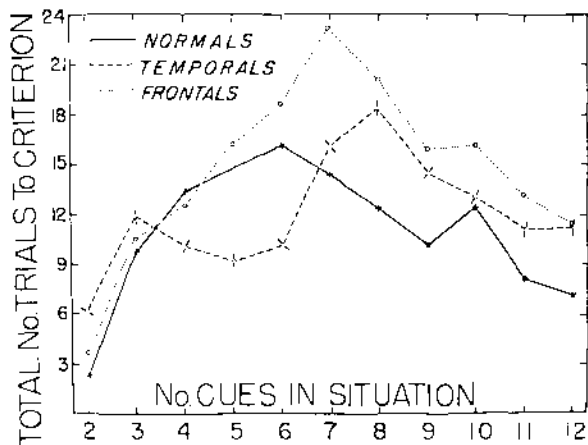
FIG. 10. Graph of the average total number of trials taken in the multiple object experiment by each of the groups (Control = *Normal*; Posterior Intrinsic Lesion = *Temporal*; Frontal Intrinsic Lesion = *Frontal*) to reach, in each of the situations, a criterion of performance of five consecutive correct responses. A correct response occurred when the monkey moved the object under which a peanut had been placed for that trial. In a succession of trials, the peanut remained under one of the objects until criterion performance was reached. Then the peanut was shifted to one of the other objects in the situation and the trials resumed; this procedure was repeated until each of the objects in each of the situations had been the correct one. (See also the legends to figs. 4, 5, and 6.)

between receptor and central mechanisms preclude an understanding of the one without an appreciation of the other. The importance of central regulation of receptor events is attested by the findings of recent physiological experiments which demonstrate mechanisms that allow the regulation of afferent activity through efferents from the central nervous system: the effect of electrical excitation of γ-efferents (one third of the fibers in the ventral spinal root) in modifying the activity of afferents originating in muscle spindles (21, 22, 67); the influence of excitation of efferents in the otic system on afferent activity initiated by auditory stimulation (36); and similar effects in the optic (19, 46), somatic (47, 54) and olfactory (60) systems. (These mechanisms are discussed in detail in Chapter XXXI by Livingston.)

'Stimuli' are thus conceived as centrally regulated receptor events. To avoid confusion, the term 'input' is reserved for those receptor events which can be shown to be systematically related to an ensemble of environmental events. Inputs are specified either by direct observation of the effects of environmental events on receptor events, or indirectly from such effects on the behavioral responses of the organism.

As with the term 'stimulus,' several uses of the term

'response' are also often confounded. As used in this presentation 'response' denotes any dependent variable which is selected as representative of an action, a repertoire of responses which can be shown to be systematically related. Movements of smooth muscle and endocrine events comprise the effector components of action; those components that modify receptor activity (i.e. the stimulus components) are referred to as the 'outcome' of actions. Actions are specified either by direct observations of the outcomes of muscular or endocrine events (e.g. the changes in the activity of afferents from muscle spindles) or indirectly from some behavioral response (e.g. the record of depressions of a lever) made by the organism. The obviously circular relation between all of these definitions is tolerable since each term is independently as well as circularly definable, the environmental terms by physical methods, the organismic terms by biological methods.

Behavior observed to be a function of systematic variations of input is referred to as 'differentiative.' Behavior observed to be a function of systematic variations of outcome is referred to as 'intentional.' Problem solution in all instances involves both differentiative and intentional behavior—however, analysis is profitably focused on each in turn.

Some Experiments

Returning to the multiple object experiment, figure 10 graphs the average of the total number of trials taken by each group of monkeys in each situation to reach the criterion of five consecutive errorless responses. The peculiarities of the shape of the curve representing the performance of the posteriorly operated animals have already been analyzed. The difficulties in performance encountered by the frontally operated group are more clearly demonstrated by comparing the graph of the total number of trials (fig. 10) with one that portrays performance following completion of search, i.e. after the first response in which the peanut is found (fig. 11). Note that the lag shown by the frontally operated group in reducing the number of trials taken to reach criterion (or the number of repetitive errors made) occurs after the peanut has been found (fig. 11). This group of monkeys experiences difficulty in attaining on successive trials the strategy of returning to the object under which on the previous trial they have found the peanut. Whatever may be the explanation of this difficulty, a precise description can be given: for the frontally operated group, 'finding the peanut' does not determine
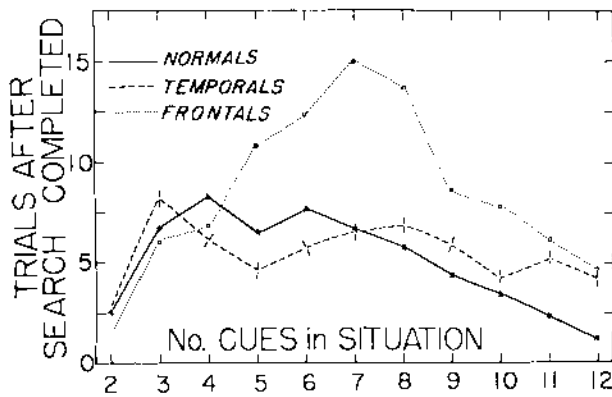
FIG. 11. Graph of the average of the number of trials to criterion taken in the multiple object experiment by each of the groups in each of the situations after search was completed, i.e. after the first correct response. (See legends to figs. 7 and 10.) Note the difference between the curves for the controls and for the frontally operated group, a difference which is significant at the .05 level by an analysis of variance. (F = 8.19 for 2 and 6 df), according to McNemar's (85) procedure performed on normalized (by square root transformation) raw scores.

subsequent choices to the extent that 'finding the peanut' determines subsequent choices for the normal group. The experimental behaviorist, using terms identical to those used by Sherrington in his lectures on 'the integrative action of the nervous system,' would describe the finding in more technical language: for the group with frontal lesions, response to the 'positive element,' i.e. the object with the peanut under it, is inadequately 'reinforced' by the finding of the peanut; as a result, the monkeys with frontal lesions do not shift their responses to the reinforced object as readily as do the controls. To state this more generally, when given a choice, the intentions of animals with frontal lesions are guided less than those of controls by the behaviorally relevant consequences, or 'outcomes,' of their prior actions.

Interestingly, before the frontally operated group begins to attain the necessary strategy (after the seven cue situation), performance of this group reflects the number of alternatives in the situation. This finding suggests a parallel with analyses of the determinants of intentions developed in the theory of games and economic behavior (141). Intentions are determined by two classes of variables: a) the dispositions of the organism and b) an estimate about the actions of other parts of the system. The finding that performance of the frontally operated group is related to the number of alternatives in the situation suggests that this group is deficient in evaluating the second class of variables

but this is only suggested by these results. Support for the hypothesis that frontal lesions do not affect the dispositional variables that determine the preferences comes from the results of another experiment.

In a constant (fixed) interval experiment, 10 rhesus monkeys are tested in an 'operant conditioning' (130) situation which consists of an enclosure (discarded icebox) in which a lever is available to the monkey. Occasionally, immediately after a depression of a lever, a pellet of food also becomes available to the monkey. The experimenter schedules the occasions on which the action of pressing the lever will make a food pellet become available. In this experiment, these occasions recurred regularly at a constant (fixed)
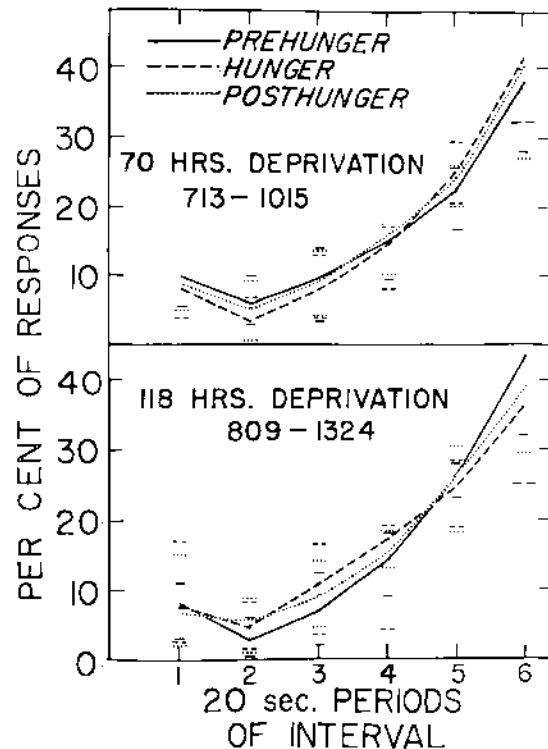

FIG. 12. Graph showing the effect of food deprivation on monkeys' rate of lever-pressing response to food (a small pellet of laboratory chow) which became available every 2 min. The change in total rate is indicated by *numbers* under the deprivation label. The lack of change in the distribution of responses is shown by the *curves*. Each curve represents the average of the responses of 10 monkeys; each point represents the average rate during a period of the interval over 10 hr. of testing. Variance is indicated by the *short horizontal bars*. (Dr. Nathan Azrin made this experiment possible by constructing apparatus and by suggesting that separate counters be used to record performance during each period of the interval. Mr. David Nowel, Mr. Thomas Tighe and Miss Libby Fleisher helped carry out this and the experiment reported in fig. 13.)
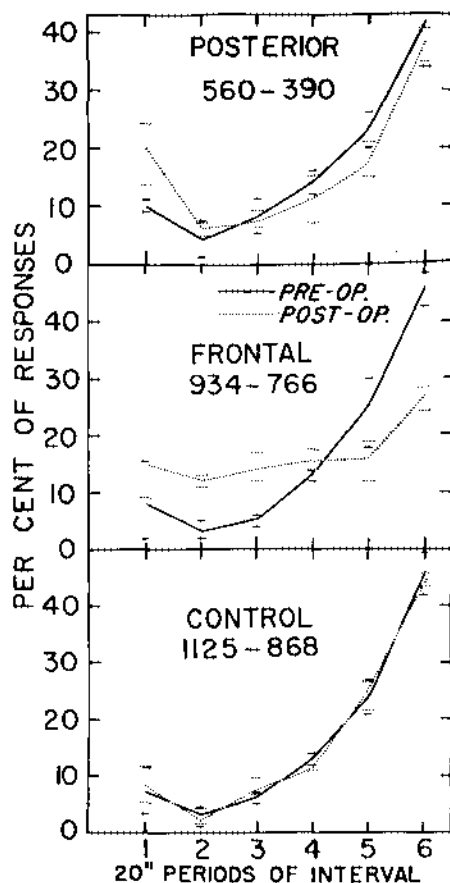
FIG. 13. Graph showing the change in distribution of monkeys' response rate following frontal intrinsic sector ablation (three monkeys). Note that the distribution of rate over the interval is not affected in the controls (four monkeys) and after posterior intrinsic sector ablations (three monkeys). Also note that the total rate of response (*numbers* below names of groups) did not increase; rather that rate was somewhat decreased, probably due to the ad libitum feeding period which all groups were given prior to operation—approximately 2 wk. before postoperative testing. (Compare with fig. 12 and see legend to that figure.)

interval of 2 min. The conditioning procedure as a rule results in performance curves (scallops) which during the early portions of the interval reflect a slow rate of response, and during the latter portions an accelerating rate which nears maximum just prior to the end of the interval. All of the monkeys used in this experiment were trained every other day for 2-hr. sessions until their performance curves remained stable (as determined by superimposition of records and visual inspection) for a least 10 consecutive hours.

Two experimental conditions were then imposed, one at a time: *a*) deprivation of food for 72 and 110 hr., and *b*) resection of frontal and posterior intrinsic

cortex. Food deprivation increases the total rate of response of all animals markedly but does not alter the proportion of responses made during portions of the interval (fig. 12). Resection of the frontal intrinsic sector does not change the total number of responses but does alter the distribution of responses through the interval—there is a marked decrease in the difference between the proportion of responses made during the various portions of the interval. Monkeys with lesions of the posterior intrinsic sectors and unoperated controls show no such changes (fig. 13).

Analysis of Results

The results of the constant interval experiment support the contention that the effect of an outcome of an action is influenced by variables which can be classified separately. Deprivation influences total rate of response; frontal lesions, the distribution of that rate. Deprivation variables are akin to those which have in the past been assigned to influence the disposition of the organism. The frontal intrinsic sector lesion appears to influence the monkey's estimate of the situation. This finding is thus in accord with that obtained in the multiple-object problem. Both experimental findings can be formally treated by the device of 'mathematical expectation' (140). The distribution of responses in the constant interval experiment can be considered a function of the temporal 'distance' from the outcome; distribution of response probabilities in the multiple-object experiment is a function of the number of objects in the situation. Frontal intrinsic sector lesions interfere with those aspects of intention that depend on an estimation of the effects that an outcome of an action has in terms of the total set of possible outcomes that are available. The effects of frontal intrinsic sector lesions on behavior related to outcomes thus parallels the effects of posterior intrinsic sector ablations on behavior related to inputs. A general model of intrinsic sector mechanisms seems therefore to be possible. As a step, after a brief review of available data, a model of the frontal intrinsic mechanisms is proposed.

Review of Other Data

The effect of frontal intrinsic sector resection on the distribution of responses in the multiple-object and constant-interval problems is correlated with other deficiencies in preferential behavior that follow such resections. The most clear-cut deficiency is in the per-

formance of delayed reaction and of alternation by subhuman primates. These problems are usually classified with those used primarily to study differentiative behavior, although differences between the two are recognized. These differences have been conceptualized in terms of one-trial learning (99), immediate memory (56) and retroactive inhibition (83), conceptions which are insufficiently distinctive to account for recently reported experimental findings (94). More penetrating analyses have been accomplished for the effects of frontal intrinsic sector lesions on the performance of the double alternation problem (78) and for the simple alternation problem per se (6a). These analyses emphasize the recurrent regularities which constitute the alternation problems and suggest that such problems be considered examples of a larger class which can be distinguished from problems that require differentiation (37). Delayed reaction may also belong to the class of problems specified by recurring regularities; the recurrence, at the time response is permitted, of some of the events present in the predelay situation, constitutes an essential aspect of the delay problem (94).

The reasons for classifying the delayed reaction and alternation problems with those related to systematic variations of outcomes remain somewhat obscure. The results of the following experiment provide some clarification. Under special conditions, monkeys with lesions of the frontal intrinsic sectors perform remarkably well the delayed reaction and alternation problems (93, 94). Adequate performance is established, however, at the cost of a great number of repetitive errors (though not of initial errors), as shown in figure 14. These results can be described as a failure in performance due to the relative inefficacy of the outcome of the frontally operated animals' actions in determining subsequent action. This description is compatible with the finding that, in delayed reaction, the important determinant of performance is the outcome of the animal's reaction in the predelay situation (94), the outcome having 'acquired distinctiveness' during the earlier phases of the experiment.

MODEL OF FRONTAL INTRINSIC MECHANISM

From these data, a formal model of the neural mechanism that underlies the effect of frontal intrinsic sector resections of intentional behavior can be proposed. This model takes into account the neural relationship between the frontal intrinsic sector and
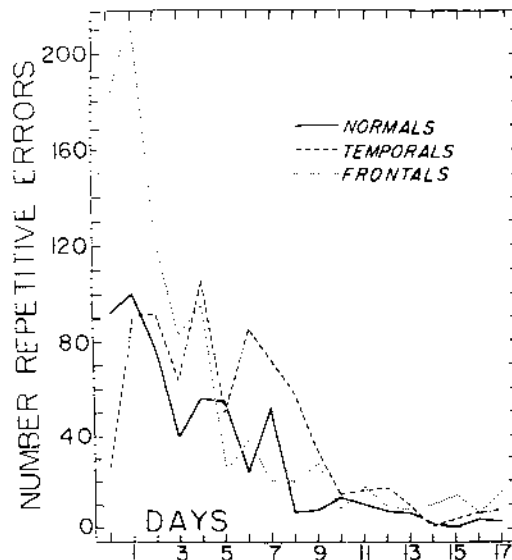

FIG. 14. Graph showing the differences in the number of repetitive errors made by groups of monkeys in a 'go-no-go' type of delayed reaction experiment. Especially during the initial trials, frontally operated animals repeatedly return to the food well after exposure to the 'nonrewarded' predelay cue. 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 (figs. 6 to 11) served as subjects some 2 years earlier in the delayed response experiment portrayed here. (Dr. Margaret Varley assisted in the performance of the earlier experiment.)

the mediobasal structures of the forebrain (110) and is based on the finding that two classes of variables determine the effects of an outcome of an action. A large body of data has been accumulated in the last 20 years as a result of studies which made use of surgical ablation and electrical stimulation. These data demonstrate the special relation of the mediobasal systems of the forebrain to the class of variables subsumed under the rubric 'disposition.'

Mediobasal Forebrain and Disposition

Changes in the following types of behavior are reported to result from mediobasal forebrain ablations and stimulations: fighting (dominance, reaction to frustration); fleeing (escape and avoidance); feeding (appetitive, such as hoarding, and consummatory); and mating and maternal (nest building and care of the young). Stimulation or ablation which affects one of these behavior patterns is likely also to affect the others (though not necessarily to the same extent). On the other hand, the performance of discrimination tasks remains unaffected (107).

Typically the damage or stimulation of mediobasal sectors affects intentional behavior by disrupting the more or less orderly recurring sequences of actions which constitute feeding, fighting, fleeing, mating and maternal behavior. None of the elements of the sequence drop out; rather the duration of any one such element of action is altered. The outcome of an action appears, in these damaged animals, to be an ineffective terminant or maintainant of acts in the sequence (18). Specifically, animals with mediobasal forebrain resections continue feeding long after control subjects (with the same amount of deprivation and in the same situation) have stopped eating (34, 111). The duration of avoidance behavior is shortened: thus, a monkey will repeatedly grasp a flaming match even though he is burned each time (35). A fighting reaction is not maintained. An animal with a mediobasal lesion may draw blood or have a finger bitten off and within a few seconds sit unconcernedly munching peanuts. This effect, as that on avoidance, is especially easy to discern in measures of extinction (117). Reactions to a 'frustration situation' are also altered along this dimension: the intensity of an animal's reaction to frustration is unimpaired, but the duration of the reaction is shorter than that of a control subject (113). When closely examined, the effects of mediobasal forebrain ablations on hoarding (133), mating (34) and maternal (134) behavior, are on the duration of a particular element of the sequence, for example, food or an infant is dropped before the nest is reached or, occasionally, carried to the nest and then taken out again to be dropped elsewhere.

The neural mechanisms whereby the mediobasal sectors affect the outcome determinants of behavior are only beginning to be detailed (109). Essentially, the mediobasal forebrain structures are especially related afferently and efferently to medial mesencephalic and diencephalic structures in which are located the slowly adapting receptors surrounding the third and fourth cerebral ventricles (such as the osmo- and temperature-sensitive elements) as well as to the nonspecific diffuse systems. The latter are characterized by networks of short fine-fiber neurons. In such networks synaptic, dendritic and electrotonic phenomena, especially sensitive to neurochemical influences, are most likely of greater total significance than are rapidly propagated patterns of neural impulses. In fact, the connections between the mediobasal forebrain and medial mesencephalic and diencephalic structures are so arranged that even when propagated signals are transmitted, the effect on the target site is more often a change in local excitability than the firing of neurons (44).

Characteristic interactions between the functions of the mediobasal sectors and those of the diffuse nonspecific systems are thus clearly established at the neural level—interactions which can account for the finding that intentional behavior is affected when mediobasal forebrain structures are ablated or electrically excited. An analysis of the effects of these interactions can therefore be undertaken. Changes in the excitability of these neural mechanisms have been correlated with changes in activation, such as sleep-wakefulness, which in the intact organism are cyclic processes. Whether the outcome of any particular action is desirable or not is a cyclic function—for instance, a heaping plate of food is most desirable at the peak of the appetitive cycle but slightly nauseating just after consumption of a large meal. The differences in the effects of outcomes depend therefore on the dispositions of the organism that are only partially (and inadequately) described by the differences that can be found to occur during any one cycle (27, 28, 48, 77, 118). More complete description would take into account cyclically recurring regularities.

The cycles of activation (or deactivation) in behavior that occur with changes in the excitability of the central system are analogous to conversions between potential and kinetic energy in physical systems—the activity of water at the base of a fall is not properly described in terms of the differences between the 'amount' of energy which exists in the limpid pool at the top of the falls and that which characterizes the excited turbulence at the base. Rather, the difference is measured by reciprocally related quantities—kinetic and potential, in the case of physical systems (such as the waterfall); or anabolic and catabolic, in biological descriptions. Thus, a 'need-reduction' formulation, in which the referent against which change is specified is considered to be some basal (that is minimal) level is inadequate. This conceptualization, by insistence on 'amount' of need as the basic variable, easily falls into the trap of confusing the reciprocally related potential and kinetic manifestations of the energic process with quantitative differences in the total amount of energy in the system.

An added argument against simple need 'reduction,' based on the notion of 'physiological need,' is that such a notion does violence to physiological fact. Oxygen deprivation produces little increase in respiratory rate, provided a constant partial pressure of carbon dioxide surrounds the respiratory receptor

mechanisms in the carotid body and brain stem (87). Food deprivation, as in starvation, is insufficient per se to increase appetite. Long-term deprivation of mating leads as often to continence as to frustration—these examples suffice to suggest that physiological need is not invariably produced by deprivation. And, of course, the converse also holds, in that 'need' (as measured by the rate or amount of movement related to an outcome) may actually increase when recurrently 'satisfied' (77).

On the other hand, the more complete specification that takes into account the reciprocally related recurring changes in the distribution of excitability and rest is supported by physiological fact. The electrical activity of totally isolated neural tissue is cyclical (7). The period of cyclical activity can be specified and any changes imposed on the normal periodicity can be described. The advantages of such description are: the 'amount of excitability' is not confused with 'amount of energy'; a particular event may increase excitability at one time, and may decrease it at another; thus, the effect of an outcome of an action is conceived to depend on the phase of the excitability cycle at the moment of action. The disposition of an organism is therefore a basic determinant of intentional behavior. Dispositions are conceived to be dependent on changes in the periods of neural excitability cycles.

Mechanism of Expectation

By analogy with the model describing the functions of the extrinsic and posterior intrinsic mechanisms, the proposal of a model of the frontal intrinsic and mediobasal forebrain mechanisms begins with a statement of the variety of transformations of descriptions of the outcome under which behavior remains invariant. Following extensive bilateral resections of the mediobasal systems, behavior remains invariant over a wide variety of transformations of outcome, for example, even gross changes in the amount of food deprivation minimally alter rate of response to food (147).

Frontal intrinsic sector lesions affect intentional behavior that remains invariant only under the more restricted ranges of transformations of the outcome, transformations which in controls can be shown to affect the distribution of intentional responses. In the extreme, unique distributions, such as those measured by indifference functions, would be most affected by such lesions.

Unique distributions can occur only when both the units of intention and their referent have been fixed. Difficulties in defining such units and their referent stem from the cyclical variations which describe the dispositions of organisms—difficulties already discussed from the neurobehavioral standpoint. The formal device 'mathematical expectation,' which is so usefully applied to the analysis of the effects of frontal intrinsic sector lesions, is designed to overcome the difficulties encountered in analyzing the solution of problems characterized by cyclic phenomena (141). This device, based on combinatorial (equilibratory) and set theoretical methods, meets the difficulties by the suggestion that the solution of such problems is described, not by the single elements (outcomes) that define the problem, but by sets (and subsets) of such elements. Unfortunately, the mathematics falls somewhat short of accomplishment in this area and only some rudimentary approaches to the task are possible at this time (142).

Nevertheless, the relevance of the device, mathematical expectation, in the analysis of the results of the multiple-object and constant-interval experiments, suggests the formal model of the frontal intrinsic mechanism. This model conceives the frontal intrinsic mechanism to partition the events in the mediobasal forebrain systems, dispositional events that determine the effect of outcome variables. Partitioning results in distributions of intentions, intentions determined by the elements of the subset resulting from the partition. The frontal intrinsic mechanism is thus conceived to provide both referent and units although not the elements that specify intentional behavior. The effect of continued frontal intrinsic sector activity will, according to this model, result in an increasingly complex sequence of distributions of intentions which in turn allow more and more precise specifications of intent that can be conveyed for any given outcome. As a result, the organism's intentional behavior remains invariant under a progressively narrower range of systems of transformations of outcomes—intentions become more precise.

The programing of the activities of the frontal intrinsic sector remains in question. Some things are clear, however. The advantage of the model is that the program is not composed by the events upon which the program operates. Thus, as in the case of the posterior intrinsic mechanisms, storage of encoded programs is demanded—not storage of an ever-increasing number of discrete preferences. In this formulation, the frontal intrinsic sector is conceived as a programing mechanism that maps intentions— a conception that is in accord both with experimental

finding and clinical observation (23, 32, 101, 103, 127).

SUMMARY AND CONCLUSION

Evidence has been presented to support the conception that the posterior and the frontal intrinsic systems serve different aspects of the problem-solving process. The argument has been forwarded that two major classes of behavior can be distinguished, differentiative and intentional. The multiple object experiment detailed above provides a paradigm of the relation between each of these classes in problem solution. Posterior intrinsic sector resection interferes with differentiative behavior during search; such lesions affect the delineation of a problem. Frontal intrinsic sector resection interferes with intentional behavior after search is completed; such lesions affect the economic solution of a problem.

Furthermore, the experiment presented shows that the delineation and economic solution of a problem can occur more or less haphazardly. Haphazard problem-solving behavior is described by the relatively wide range of systems of transformations of the input and outcome under which behavior remains invariant. Strategic problem solution, on the other hand, occurs with restriction of the range of such systems of transformations. The experiment is interpreted to indicate that restriction in this instance results from the operation of a mechanism (the intrinsic) that partitions the neural events (in the extrinsic and mediobasal forebrain systems) determined by input and outcome. By providing both a referent and units, partitioning defines the range of possibilities to which an input or outcome is assigned by the organism.

The distinction between neural mechanisms that serve differentiation and those that subserve intention is not a new one. Sherrington makes this distinction in his description of the coordination of reflexes (129): The "singleness of action from moment is the keystone in the construction of the individual." This singleness of action comes about in two ways—'interference' between and 'allied combinations' of reflexes. In his analysis of 'interference' (or antagonism) between reflexes, Sherrington forwards concepts such as inhibition, induction and spinal contrast—concepts which have relevance to discriminative behavior [for example, as already noted, the use of the concept 'induction' by Skinner (130) for the occurrence of the 'hump' in the graphical representation of complex discrimination learning].

Sherrington uses these concepts to provide an understanding of the differences between reflex behaviors to different inputs. On the other hand, Sherrington's discussions of 'allied combinations' of reflexes are an attempt to understand behavior regulated by outcomes: "the new reflex breaks in upon a condition of equilibrium, which latter is itself a reflex," a notion which has been enlarged upon by Cannon (9) and more recently by Wiener (151). In discussing allied combinations of reflexes, concepts such as reinforcement, convergence, summation and facilitation are used by Sherrington—concepts which have relevance to intentional behavior.

More recently, Denny-Brown (17) has distinguished between cortical resections that affect patterns of approaching (grasping, hopping, placing) and those that affect patterns of avoiding (withdrawing). Although the cortical resections made by Denny-Brown and those described here are only roughly comparable, enough correspondence exists to permit the suggestion that the patterns of approaching and the sampling of inputs as described here may reflect some common mechanism, that the patterns of avoiding may be manifestations (in untamed animals subjected to laboratory routines) of the behavior described here as guided by outcomes.

The neural mechanism here proposed is similar in some respects to others already formulated. The neurobehavioral data presented, and their formal analysis, suggest that the events in the extrinsic and mediobasal forebrain systems are indeed the important determinants of moment-to-moment behavior as in Lashley's (72) and in Köhler's formulations (63 65), among others. However, these events are acted upon by others which provide the contextual matrix that sets limits on the moment-to-moment behavior, as proposed by Freud (33) and more recently by Forgus (29-31). The resultant of the interaction of these two classes of neural events is described more formally, though less picturesquely, by the mechanism, 'partitioning of sets,' than this resultant is described by Lashley's largely nativistic or Hebb's largely empiricistic conceptions: reduplicated neural loops (69) or phase sequences (53). Yet all three share the essential characteristic that, in continued problem-solving behavior, increasingly complex patterns of neural events occur, patterns that allow more and more precise differentiations and intentions to be made.

Nor is the distinction between the delineative and the economic aspects of problem solution a new one in the behavioral sciences. The contributions of the

Würzburg school (55) and their Gestalt-oriented successors (2, 62, 149) have consistently emphasized the distinction between the 'content' of thought and its 'motor'; between knowledge and intention (62). These formulations, however, frequently confounded two of the pairs of distinctions made in this presentation: the distinction between the delineative and the economic aspects of problem solution on the one hand and, on the other, that between the attitudinal (partitioning) factors and the events upon which these attitudes operate. Piaget (104) comes somewhat closer to maintaining separate these distinctions. This correspondence between Piaget's analysis of the results of his experiments and that presented here may be due to the similarity of the formal devices used: Piaget's 'groups of displacements' are included in the 'systems of transformations' referred to throughout this presentation.

Social scientists have also made use of the distinction between the delineative and the economic aspects of problem solution. Thus, Parsons distinguishes between determinants of 'interest' in a problem and those of 'value-orientation which provide the standards of what constitute satisfactory solutions of these problems' (100). Basic to this distinction is the difference as yet grasped only vaguely, between the acquisition of information (128) and its utilization (140–142). The development of this distinction in the social, as well as in the biological (and in the physical) sciences, is hampered by the fact (already mentioned above) that, in connotative use, the language of occidental cultures fails to separate clearly the differences brought out by the neurobehavioral analysis made here: differences between attitudinal factors and the events upon which these attitudes operate on the one hand, and between the delineative and the economic aspects of problem solution on the other. Recently, there has been in North America a shift in popular connotation away from attitudinal determinants—e.g. the term 'honesty' no longer refers exclusively to 'telling the truth,' 'respecting others' property' and such, but also to 'behaving according to how one *feels* and *sees* the situation,' even if this entails occasional lying or stealing (119). Such confusion in connotative meaning creates

especial difficulties for a science that must obtain data almost exclusively from verbal reports. The results of analyses such as this one of neurobehavioral data may be most usefully applied to the social sciences as keys that open avenues of conceptualization common to all sciences—conceptualizations now locked behind the intricacies of verbal behavior.

We thus, from the biological standpoint, see the cerebrum, and especially the cerebral cortex, as the latest and highest expression of a nervous mechanism which may be described as the *organ of, and for, the adaptation of nervous reactions.* The cerebrum, built upon the distance-receptors and entrusted with reactions which fall in an anticipatory interval so as to be *precurrent . . .* , comes, with its projicience of sensation and the psychical powers unfolded from that germ of advantage, to be the organ *par excellence* for the readjustment and the perfecting of the nervous reactions of the animal as a whole, so as to improve and extend their suitability to, and advantage over, the environment. . . . Only by continual modification of its ancestral powers to suit the present can it fulfil that which its destiny, if it is to succeed, requires from it as its life's purpose, namely, the extension of its dominance over its environment. For this conquest its cerebrum is its best weapon. It is then around the cerebrum, its physiological and psychological attributes, that the main interest of biology must ultimately turn.

SHERRINGTON, C. S. *The Integrative Action of the Nervous System,* p. 390 (129).

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