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Comparative Neurology and the Evolution of Behavior [*]

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> The rules established for localization of function in the brain can best be demonstrated by example. The first structure, which naturally belongs amongst the most important, is the structure dealing with sexual activity, i.e. reproductive functions. The following evidence attests to the proposition that these functions are served by one particular part of the brain: It is larger in those species possessed with greater sexual vigour; it is larger in males than in females (a corollary of the fact that activity is cyclic in the female); after castration or in old age, the structure becomes smaller as the skull increases in thickness. Additional evidence comes from clinical cases where priapism and satyriasis are frequently observed in patients with cervical pathology. The author knew a man in Vienna whose sexual activities were remarkable. This man was so uninhibited and insatiable that he must have six women, one after the other, to satisfy him. Postmortem, this man's cerebellum was found tremendously enlarged. (Gall, 1807, translated and paraphrased.)

> So far as the functions of the gyrus cinguli are concerned, experimental evidence is scant, owing to the inaccessibility of this region. I have noted ("The Brain of Helen H. Gardener, Alice Chenoweth Day," *Amer. Jour. Phys. Anthropol.*, II; 29–79, 1927) that in the two sexes the precuneous shows a greater difference in size than any other portion of the cortex, being more highly developed in the male, and it was suggested that representation of the sex organs may be localized there. This difference between the sexes has been confirmed by Mettler in the brain of the monkey. Sensations related to sex matters possess a high degree of emotional coloring—there seems to be ample justification for the ancient view of La Peyronie, professor of surgery at Montpellier, who, on the basis of such clinical experiences expressed the belief that the region of the corpus callosum is the "seat of the soul." (Papez, 1937.)

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[*] The author is deeply indebted to Professor Jerzy Rose for his guidance of the anatomical studies reported. This in no way indicates, however, that Professor Rose is (or for that matter is *not*) committed to the *ideas* expressed. Discussions with Dr. Lawrence Kruger, who kindly furnished some of the illustrations used, have also been helpful—again, I take full responsibility for the views expressed.

IT IS NOT too surprising that recently an eminent student of the nervous system stated his disappointment with the contribution made by the comparative method to an understanding of cerebral function (Bailey, 1949). On the other hand, formulations such as those which propose the neural correlates of emotion on the basis of comparative anatomical material continue to excite the interest necessary to spawn experiments (Herrick, 1948; Papez, 1937; MacLean, 1949). Which of these rather diverse approaches most appropriately indicates what we might expect comparative neurology to contribute to the understanding of the evolution of behavior? My answer, to be developed by example, lies somewhere between these extremes: I believe that precise comparative data, carefully analyzed, can lead to testable hypotheses concerning the *taxonomy* of behavior; that by observation and experiment such hypotheses can then be tested and the resulting data systematized. These systematic taxonomic schemes then serve as a base for further hypotheses—both at the neural and at the behavioral level—and the observation-experiment-systematization cycle repeated. This approach provides the flexibility which is lacking in *systems of hypotheses* (implicit or explicit) and avoids the nihilism of disappointment resulting from the collapse of such systems when they become sufficiently awkward under the impact of new data.

This approach is not without difficulties, however. As an example of the pitfalls posed, I can tell a story on myself. A specific behavior pattern can be mediated by different neural mechanisms in different species. In studying the functions of the so-called silent areas of the primate cerebral cortex, two behavioral tests have proved especially valuable: the choice reaction, in which an animal chooses one of two *disparate* objects in order to receive a reward, and the delayed reaction, in which the rewarded choice is between *like* objects which are differentiated by some prior signal. Failure to perform these tasks had provided a reliable index of damage to two circumscribed portions of the primate cerebral mantle (the anterofrontal and inferotemporal cortex). Since one of these portions (the frontal) has been referred to by the lofty title "the organ of civilization" (Halstead, 1947), it is not too surprising that, in spite of repeated warnings to myself, I had inadvertently come to view such tasks as measures of some especially high and noble functions. Of this delusion I was quickly divested one afternoon when, to my surprise, I watched *pigeons* (Ferster and Skinner, 1957) perform these and many other more complex tasks as well as, and in some respects better than, my primate relatives. And when I saw and heard that even the octopus (Young, 1953) could perform tasks which had been invented to demonstrate that children and animals had ideas, I had to face the fact that, though monkeys deprived of cortical tissue might experience grave difficulties with such tasks, nonmammalian species manage their affairs remarkably well without a cerebral mantle. The descriptive term "encephalization," used to cover these facts, does not help much in elucidating the problems of cerebral function or those of classification of the behavior exemplified by these "choice" tasks. Nor does it temper an overly enthusiastic evaluation of the importance of the particular neural mechanism and of the behavior patterns it serves.

The task of relating the evolution of any given behavior pattern to the development of neural structure is little different from that of relating behavior patterns to other anatomical entities: two organisms may use phylogenetically unrelated structures to accomplish apparently similar behaviors (analogy); of more interest to us, structures which can be shown related by comparative morphology *may* serve patterns of behavior which superficially appear to have no common element (homology). More often than not, the neural structures involved have undergone some changes (e.g. enlargement, rotation, altered configuration); in addition, the behavior patterns to be compared are frequently ill defined or may even be completely unstudied in one of the species under consideration. Thus, the congruity or disparity of the behavior remains in question until techniques are devised which test *comparable* behavior in both species—this in turn is dependent on a fairly thorough understanding of the behavior patterns under investigation. Why, then, this effort? The assumption underlying such endeavor is that the several behavior patterns served by homologous neural structures *share some common element.* Thus, uncovering a behavioral process which, in spite of superficial modifications, is shown to depend on homologous neural structures provides a valid criterion useful in a taxonomy of behavior —and valid criteria for classification are not abundant in the behavioral sciences. The demonstration of such constancies can then be utilized as the backdrop against which the evolutionary changes (designated above as "superficial") can be understood.

My presentation has the following central thesis: Until now, comparative neurological data have been used in very specific ways to support the notion that certain behavior patterns are innately determined while other patterns are predominantly the result of experience. The argument has been made that innately determined "instinctive" behavior patterns are served by neural mechanisms which are uniform throughout phylogeny; that the neural mechanisms serving "learned" behavior vary considerably among phyla, reaching their maximum development in primates. Furthermore, the difference in forebrain structures which has been invoked to support this characterization of the dichotomy between "instinct" and "learning" has been the difference between paleo- and archipallial formations on the one hand and neopallial formations on the other. I plan to show that this particular formulation is in error (see also Beach, 1952). In its place I propose that a more useful distinction is described between an internal core and an external portion of the prosencephalon; that the internal core is primarily related to changes in central nervous system excitability; that the external portion serves propagation of patterns of signals; that the internal core is primarily concerned in mechanisms necessary to the performance of behavior sequences while the external portion is related to informational processes necessary in discriminative behavior. *Each* of these major divisions of the forebrain has "old" *and* "new" subdivisions; each of the classes of behavior (sequential and discriminative) is *both* innate and experientially modifiable.

THE VERTEBRATE FOREBRAIN

Although an undifferentiated forebrain (prosencephalon) is recognizable in *prevertebrate chordates* (Cephalochordata, e.g. *Amphioxus*), the characteristic division of the vertebrate brain into telencephalon, diencephalon, mesencephalon, metencephalon, and myelencephalon is found in primitive vertebrates (cyclostomes, e.g., lampreys) and is considered prototypical of that of all other vertebrates. In *cyclostomes* the telencephalon has two "cerebral hemispheres"; the diencephalon is divisible into hypothalamus, thalamus proper, and epithalamus—however the thalamus proper is not well developed, especially in its dorsal portion. Still greater differentiation of the forebrain can be observed in the *cartilaginous fishes* (elasmobranchs, e.g. dogfish, skate, shark).

The telencephalon is enlarged both in its basal (striatal and septal) portions and in its roof (pallium). In addition to the diencephalic divisions noted in cyclostomes, the thalamus proper is subdivided into a ventral and a dorsal portion. The primitive pallium of the cartilaginous fish differentiates further in two directions: (1) In certain of the *bony fish* (ganoids and teleosts) paleopallial and archipallial rudiments, though discernible, are not as prominent as a hypopallial (also called neostriatal) formation which results from an exversion of the cerebral mantle increased through ventral growth. (2) In amphibia a primordial archipallium is overshadowed by the development of the paleopallium through medial growth of the cerebral mantle over a thickened septum, amygdala, and paleostriatum; rudiments of a general cortex are recognizable. Concurrently, the amphibian dorsal thalamus enlarges considerably. Thus, the major divisions of the vertebrate prosencephalon are clearly discerned in all tetrapods.

The differentiation of the prosencephalon is even more apparent in the reptiles (and birds) and culminates in mammals. The reptilian (and avian) telencephalon emphasizes the archipallium over the paleopallium and general cortex; in mammals the general cortex assumes ascendancy. In the reptilian (and avian) diencephalon, the dorsal thalamus differentiates recognizable internal and external portions. The internal portion is composed of central, medial (n. rotundus) and anterior nuclear masses; the external portion, of a ventral nuclear mass (n. dorsolateralis anterior), a posterior nuclear mass (n. ovalis) and a geniculate complex (n. geniculatus ventralis)—and in birds a n. geniculatus medialis. A similar grouping can be made of the nuclei of the mammalian thalamus and will be discussed in detail below. (This résumé is based on Kappers, Huber, and Crosby, 1936).

COMPARATIVE BEHAVIOR OF VERTEBRATES

The broad outlines of the comparative neurology of the inframammalian prosencephalon are thus fairly well delineated: an increasing differentiation of the rostral end of the neuraxis is described as one proceeds from prevertebrate chordates through cephalochordates, cyclostomes, fishes, amphibia, reptiles, to birds and mammals. Can a parallel increase in the differentiation (complexity) of behavior patterns, or of certain classes of behavior patterns, be traced in these organisms? Precise behavioral data regarding prevertebrate chordates, cephalochordates, and cyclostomes are practically nonexistent. Precise comparative behavioral studies of fishes, amphibia, reptiles, and birds do *not* support any notions that these forms differ significantly from each other or from mammals with regard to the complexity of the total behavioral repertoire displayed. Discriminations as in mazes (Tinklepaugh, 1932; Franz, 1927; Yerkes, 1903), speed of learning (Churchill, 1916), and the duration of retention of learned responses (Goldsmith, 1914), when they have been measured, show remarkable similarity among these various vertebrates. Differences, when they do occur, are attributable to differences in peripheral receptive and manipulative structures and do not correlate with differences between the forebrains of these animals (Warden et al., 1936). Nonetheless, fundamental differences in the structure of behavior, though not as yet subjected to rigorous experimental comparisons, are noted by the comparative psychologist.

Yerkes (1904, 1905), in a series of studies, presented different auditory stimuli to a frog. Some of these stimuli (e.g. splashing water) altered the rate of respiration without any change in the overt response of the animal. If, however, the sound was shortly followed by a visual stimulus, the frogs jumped sooner than if no auditory stimulation had preceded. Other results show that amphibia may be "tensed" by one or another stimulus so that response to a subsequent stimulus of a different type may be influenced. This ability to delay a response (hesitate) represents a different type of sensory control of action from the rather inflexible immediate response to stimulation which is found in fishes. This trend toward the multiple "sensory" determination of an action is paralleled by a trend toward a multiple "motivational" determination of response—e.g. fish under the influence of factors leading to reproductive behavior are insensitive for long periods to factors which at other times lead to feeding, flight, or rest (Warden et al., 1936).

The trend toward "multiple" determination of action in these vertebrates is, at the present writing, the one generalization derived from the study of comparative behavior which correlates with the comparative neurological generalization that describes the progressive differentiation of the forebrain. This trend in behavior has, as a rule, been ascribed to the emergence of a general or neocortex in the tetrapods—I prefer to consider the differentiation of all of the diencephalic and prosencephalic structures in making a correlation. The more restricted correlation was derived from the premise that paleopallial and archipallial formations function exclusively as olfactory structures, a premise which has been shown erroneous (Pribram and Kruger, 1954). In nonmammalian tetrapods, the archi- and paleopallial forebrain structures and their diencephalic correspondents *are* the predominant new formations—new behavioral manifestations may as well be attributed to the appearance of these formations as to the appearance of a rudimentary general cortex. My plea: let us not ignore the archi- and paleopallial formations and their diencephalic correspondents by relegating to them only olfactory functions; let us keep open the possibility that the trend toward multiple "sensory" and "motivational" determination of behavior in submammalian vertebrates is correlated with the progressive differentiation of the *entire* forebrain, and not with the appearance of one or another specific structure such as the general cortex.

THE MAMMALIAN FOREBRAIN

With this introduction to the comparative evolution of the vertebrate forebrain and the possibilities of the correlation of observed structural differences to differences in behavior, let us turn to a more minute examination of the mammalian forebrain and correlations between the evolution of its structure and the evolution of behavior. The neurological truism that the key to the understanding of the forebrain is to be found in an understanding of its input is given new impetus by recent advances in neurophysiology. A most significant series of contributions has delineated differences between those systems in the neuraxis which lie close to the central canal and those more laterally placed. The systems near the central canal are characterized by many synapses, by fine, short fibers, by a diffuseness of interconnections. Those systems which are remote from the central canal are characterized by large, long fiber tracts so constituted that considerable topological correspondence is maintained between periphery and central terminus. Receptor excitation is mediated through both systems (Starzl et al., 1951). Destruction of the internally placed systems grossly alters central nervous system excitability fluctuations as measured by the electroencephalogram. Such destruction also interferes with normal activity cycles such as sleep-wakefulness, though leaving intact the organism's specific reactions to specific stimulation (e.g. turning head and eyes toward a light) (Lindsley, et al., 1950). Destruction of the more laterally placed input systems interferes with these specific reactions (mode specificity, e.g. visual, auditory, somesthetic; topographic specificity, e.g. anesthesia or paralysis of a hand, a visual field defect). The initial terminus of these various input systems in the forebrain is the diencephalon. As we have already noted, the vertebrate diencephalon early differentiates into a hypothalamus, a thalamus proper, and an epithalamus. Hypothalamic nuclei situated in proximity to the third ventricle partake of the characteristics of the diffuse "activating" input systems (Magoun, 1950); little is known concerning the input relationships of the epithalamus. The thalamus proper is our main concern. It may be divided into a ventral and a dorsal portion. The development and functions of the ventral portion (reticular and dorsolateral geniculate nuclei) are not well understood. Some experiments suggest that there is a diffuse input to the reticular nucleus and that diffuse activation or facilitation of the telencephalon results from stimulation of the reticular and dorsolateral geniculate nuclei (Jasper, 1949). Other evidence (Chow, 1952; Rose, 1950), however, suggests that the connections of the reticular nucleus with the endbrain are more specific and that no diffuse activation results (Starzl and Magoun, 1951) from stimulation of this structure. It is clear, however, that the proportion of ventral thalamic structure to dorsal thalamus is larger in submammalian vertebrates than in mammals. As the thalamus proper becomes more and more differentiated in various mammals, the increased differentiation (and increased mass) takes place exclusively within the dorsal thalamus. It is to this structure, therefore, that we turn for an understanding of the functions of the mammalian forebrain.

THE DORSAL THALAMUS AND ITS TELENCEPHALIC PROJECTIONS

The mammalian dorsal thalamus is composed of several nuclear groups which are identifiable in practically all mammalian species (Fig. 7-1). On the basis that some of these nuclei bear a fairly consistent relation to one another, an external portion and an internal core of the thalamus can be distinguished. The external portion is composed of the ventral, the posterior (lateral and pulvinar), and the geniculate nuclei. 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 (Figs. 7-1 and 2). The internal core of the dorsal thalamus may also be subdivided into three large groups: the anterior, the medial, and the central (midline and intralaminar) (Fig. 7-1).

Each of the major subdivisions (external and internal) may be further characterized according to the type of its nontelencephalic major input (Fig. 7-3). 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 optic and otic radiations) of the somatic, gustatory, auditory, and visual systems (Walker, 1938). Within the *internal core,* the anterior nuclei receive an input from the posterior hypothalamus through the mammillothalamic tract; the central nuclei receive those nonspecific diffuse afferents by way of the reticular formation of the mesencephalon, and in addition a probable input from the anteromedial hypothalamus (Morin, 1950; Morin et al., 1951). (The hypothalamus, as we have already seen, partakes of the characteristics of the diffuse systems.) Thus the constancies of morphology in the mammalian thalamus reflect certain gross distinctions which can be made in the types of input to the forebrain.

The other two nuclear groups, the *posterior* in the external portion and the *medial* in the internal core, do not receive any such major extrathalamic input and have been classified therefore as the "intrinsic" nuclei of the thalamus (Rose and Woolsey, 1949). Important to our argument, which is detailed below, is the fact that there is an *intrinsic* nucleus in *each* of the major thalamic divisions (see Fig. 7-3).

The projections to the telencephalon of the dorsal thalamus have been delineated in several mammals. The external portion of the dorsal thalamus projects to the dorsolateral and posterior cortex (Fig. 7-4). The nuclei of the internal core project to the frontal and mediobasal portions of the forebrain, including 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 (Walker, 1938; Chow and Pribram, 1956); the geniculate group to the lateral portion of the temporal and the posterior portion of the occipital lobe (Walker, 1938);

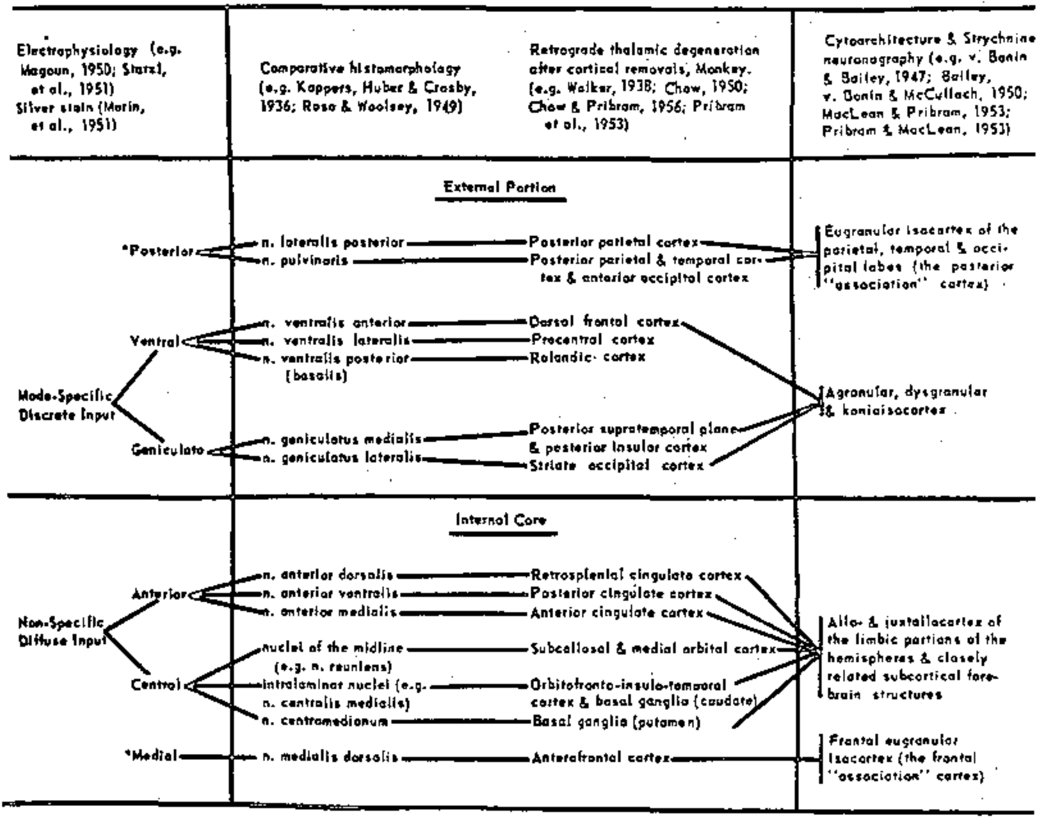

Fig. 7-3. Diagram of the distinctions between an internal core and an external portion of the forebrain. Examples of the techniques and particular studies used in making the classification are given across the top. As in any such classification, its heuristic value should not obscure its deficiencies: 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.

the posterior nuclear group to the remaining cortex of the parieto-temporo-occipital (PTO) convexity (Chow, 1950; Chow and Pribram, 1956).

Within the internal core (Fig. 7-4) the medial nuclei project to the anterofrontal cortex (or orbitofrontal, as it has been called in subprimate mammals) (Rose and Woolsey, 1948b; Walker,

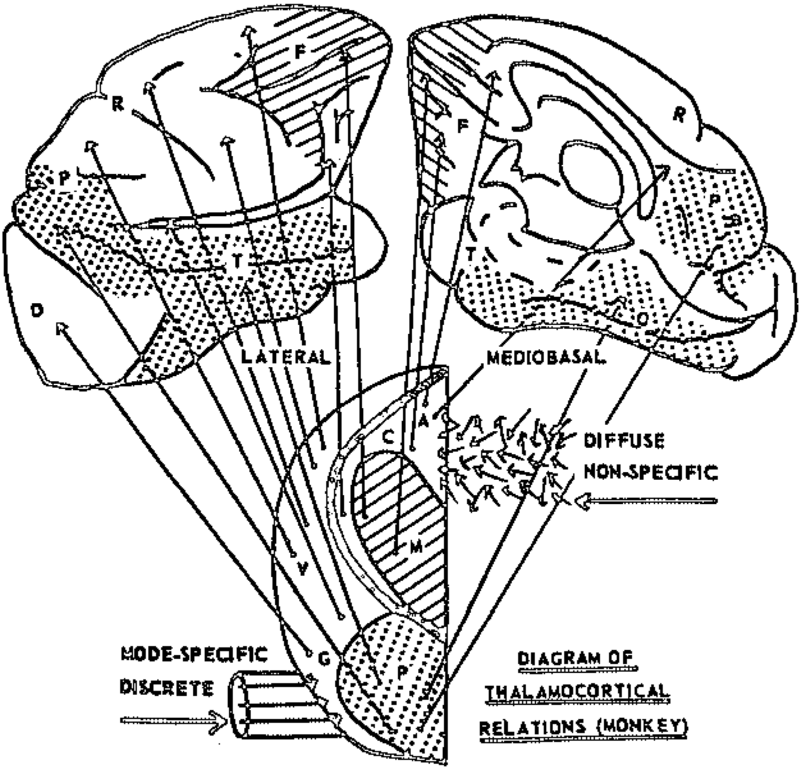

Fig. 7-4. Schematic representation of the projections from the dorsal thalamus to the cerebral cortex in the monkey. The lower half of the figure diagrams the thalamus, the straight edge representing the midline; the upper half of the figure shows a lateral and mediobasal view of the cerebral hemispheres. 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 parieto-temporo-occipital cortex. The boundaries of the cortical sectors of the intrinsic systems are not sharp and as yet are 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.

between the posterior nuclei and the ventral group is so intimate in all species that precise definition of the boundaries between them is often difficult (Chow and Pribram, 1956). Contiguity with the geniculate group is maintained posterolaterally in all mammals in spite of a marked ventral rotation of this group and its virtual separation from the rest of the thalamus in primates.

Neurobehavioral studies have shown that damage to the PTO cortex (which derives its thalamic input from the posterior nuclear group) affects the animals' ability to make choices among disparate environmental events, whether that ability has been preoperatively instilled or is investigated by postoperatively administered training procedures (Warren and Baron, 1956; Blum et al., 1950; Mishkin, 1954; Mishkin and Pribram, 1954; Pribram and Barry, 1956). Depending on the location of the damage within the PTO cortex, choices mediated by one or another sense modality are affected; thus far, no effects transcending modality have been uncovered by such experiments. Recent behavioral experiments on man (Wallach and Averbach, 1955) which demonstrate the hitherto unsuspected importance of modality-specific memories may also be mentioned in support of the hypothesis. Thus the element common to the behavior served by the external portion of the dorsal thalamus and its projection to the dorsolateral and posterior cerebral areas is some as yet poorly defined sensory mode-specific "differentiation" factor important to the solution of discrimination tasks.

Evidence contrary to the hypothesis has come entirely from studies on man. Stimulation of the temporal convexity of the cerebrum in patients suffering from epilepsy due to brain pathology and sufficiently severe to warrant surgical intervention has elicited "memories" (Penfield and Jasper, 1954). These findings have been interpreted to mean that the portion of the brain involved in such stimulations serves "memory functions" in general. It is clear, however, that in practically all cases memories in only one modality are elicited in any one patient from any reasonably circumscribed locus, and that the variable pathological involvement of brain tissue makes *inter*patient comparison of data with respect to this problem difficult. Other evidence suggests that certain portions of the PTO cortex may serve intermodality visual-somatic "spatial" orientation in man (Semmes et al., 1955; Humphrey and Zangwill, 1952). The lesions producing such "spatial agnosia" are, of course, not clearly circumscribed or defined. Nor has the suggestion that such spatial symptoms may result from a purely somatosensory defect been adequately explored, though the findings with respect to the other agnosias (Bay, 1950) urge such an exploration.

Nonetheless, these data from the clinic serve to sharpen the focus on the relevance of our problem to the evolution of behavior. Stated succinctly it is this: Does the complexity of man's perceptual processes (including the language function) evolve through the development of a supramodality or *association* mechanism or does it evolve through the development of a mechanism permitting greater *differentiation* within each modality (Gibson and Gibson, 1955)? Comparative morphology leads me to place my bet on the latter.

Systematization of morphological and behavioral data regarding the medial intrinsic nuclei and their projections to the anterofrontal cortex is somewhat more difficult. The morphological kinship of the medial nuclei with the central (midline and intralaminar) has been pointed out (Rose and Woolsey, 1948b): the medial nucleus "fuses" with the midline and intralaminar nuclei "to such a degree that their separation is sometimes artificial." Contiguity with the anterior nuclei is maintained anterodorsally in all mammals.

Neurobehavioral studies have shown that damage to the anterofrontal cortex (which derives its thalamic input from the medial nuclear group) affects the animals' ability to solve tasks in which correct solution is not determined by the concurrent environment but depends exclusively upon some prior event (Morgan and Stellar, 1950; Jacobsen, 1936; Jacobsen and Nissen, 1937; Harlow and Settlage, 1948; Harlow et al., 1952; Mishkin and Pribram, 1955, 1956). In these tasks sequential behavioral dependencies are involved and these are implicated irrespective of the modality which mediates the "prior" event (Pribram and Mishkin, 1956; Pribram, 1950).

What common element is to be found in the behavior affected by manipulations of the medial and basal telencephalon (the projection areas of the anterior and central nuclear groups) and that affected by manipulations of the anterofrontal cortex? An answer is suggested by the findings that *both* anterofrontal and medial and basal cerebral lesions (but not those of the dorsolateral

1938; Mettler, 1947; Pribram et al., 1953). The anterior and the central nuclei project to the medial and basal forebrain structures: the anterior nuclei to the limbic areas on the medial surface of the frontal and parietal lobes (Rose, 1927; Waller, 1937; Lashley and Sperry, 1943; Rose and Woolsey, 1948b; Mettler, 1947; Pribram and Fulton, 1954; Pribram and Barry, 1956). The central nuclei project (Rose and Woolsey, 1949; Droogleever Fortuyn, 1950; Powell and Cowan, 1956; Pribram and Bagshaw, 1953; Bagshaw and Pribram, 1953) to the anterior rhinencephalic and closely related juxtallocortical areas and basal ganglia (second rhinencephalic system as defined by Pribram and Kruger, 1954).

Neurobehavioral Studies (Mammals)

The elementary functions in behavior of the ventral and geniculate nuclear groups and their projections to the dorsolateral and posterior cerebral cortex will not be discussed here. Lashley's many studies in vision (e.g. 1942), and those of Klüver (e.g. 1942) and of Harlow and Settlage (e.g. Harlow, 1939; Settlage, 1939) in this modality; the studies of Ruch (e.g. Ruch and Fulton, 1935) and of Zubek (e.g. 1952) in somesthesis; those of Neff and his group in audition (e.g. Jerison and Neff, 1953); and of Patton and Ruch (1944), of Benjamin and Pfaffmann (1955), and of Bagshaw and Pribram (1953) in taste, can be referred to for summaries of this work in animals. Studies in man may be reviewed by referring to the Research Publications of the Association for Research in Nervous and Mental Diseases (1956). Essential to our argument is the demonstration by these studies that a separate thalamocortical system is involved in each of these sensory modalities.

The elementary functions in behavior of the anterior and central nuclear groups and their projections to the medial and basal telencephalon have been delineated only recently. These thalamocortical systems serve behavior which has often been classified as "instinctive," a classification which is acceptable provided the definition of instinct does *not* depend on the characteristic that the behavior is innate. (More will be said below about the appropriate defining characteristic.) Specifically, ablations and stimulations of the medial and basal telencephalon have affected feeding behavior (Pribram and Bagshaw, 1953; Stamm, 1955a; Weiskrantz, 1953); fighting or aggressive behavior (Bard and Mountcastle, 1948; Klüver and Bucy, 1939; Rosvold et al., 1954; Brady and Nauta, 1953); fleeing or avoidance behavior (Bard and Mountcastle, 1948; Klüver and Bucy, 1939; Pribram and Fulton, 1954; Pribram and Bagshaw, 1953; Schreiner and Kling, 1953; Brady et al., 1954; Weiskrantz, 1956; Pribram and Weiskrantz, 1957); mating behavior (Klüver and Bucy, 1939; Schreiner and Kling, 1953); and maternal behavior (Walker et al., 1953; Stamm, 1955b). Essential to our argument is the observation that, in contrast to the modality-specific classes of behavior described above, these behavior patterns are characterized by considerable variability with respect to the concurrent environmental situation—events in the immediate past must be taken into account in order to describe the behavior adequately. Thus, a sated animal will react differently to a food or sex object than will a deprived animal; whether fighting or fleeing will occur in a social situation will depend on a multiplicity of yet undetermined antecedent factors (perhaps amount of total stimulation); maternal behavior is not elicited in the normal nulliparous organism.

The "intrinsic" posterior and medial nuclear groups and their projections are of special interest. The morphological data that the two intrinsic thalamic nuclear groups and their projections may be assigned to two separate divisions in all mammals (and, as we have seen, even in nonmammalian tetrapods) suggest a hypothesis regarding the taxonomy of the behavior served by these structures. The hypothesis may be stated simply: (a) the behavior served by the posterior intrinsic nuclei and their projections to the PTO cortex will share some common and exclusive element with the behavior served by the remainder of the external thalamic division and its projections: (b) the behavior served by the medial intrinsic nucleus and its projections to the anterofrontal cortex will share some common and exclusive element with the behavior served by the remainder of the internal core of the thalamus and its projections. Studies generated by this hypothesis and utilizing the monkey for the most part have been under way for a decade. They have been detailed in other publications (Fulton, 1951; Pribram, 1955, and in press, a) so that a summary would be more appropriate for this occasion.

With respect to the posterior group and its projections, both the morphological and the behavioral facts are overwhelmingly consistent in support of the hypothesis. Anatomical contiguity

Fig. 7-1A. Frontal section through rostral dorsal thalamus of monkey. Note clear separation of anterior and ventral groups by fibers of the internal medullary lamina (IML).

Fig. 7-1B. Section somewhat caudal to that in Fig. 1A. Note how the central group lies within the fibers of the IML.

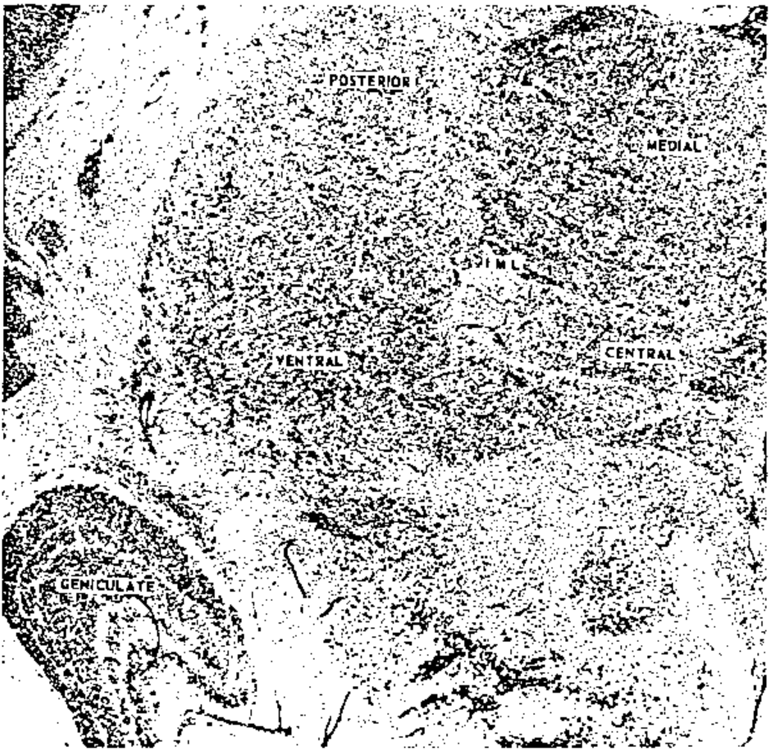

Fig. 7-2. Section about halfway through thalamus. Note the visible distinction between the internal core (medial and central nuclei) and the external portion of the thalamus (ventral and posterior groups).

and posterior convexity) markedly *shorten the duration* of an avoidance reaction (Pribram and Fulton, 1954; Pribram and Bagshaw, 1953; Brady and Nauta, 1955; Pribram and Weiskrantz, 1957). Analysis of the variables important in the deficit produced in the delayed reaction and alternation tasks by the frontal lesion (Meyer et al., 1951; Nissen et al., 1938; Finan, 1942; Mishkin and Pribram, 1955; Pribram, 1950) clearly demonstrates the importance of the animal's reaction to *the signal* which indicates the choice *subsequently* rewarded. The *duration* of this reaction has been shown to be critical (Malmo, 1942). Analysis of the effects on behavior of medial and basal telencephalic manipulations also points to alterations in the *duration* of units in the sequences involved in feeding, fighting and fleeing, mating and maternal behavior (Weiskrantz, 1953; Fuller et al., 1957; Rosvold et al., 1954; Pribram and Bagshaw, 1953; Pribram and Fulton, 1954; Pribram and Weiskrantz, 1957). Thus the element common to the behavior served by the internal core of thalamic nuclei and their projections to the anterofrontal, medial, and basal telencephalon appears to be an as yet poorly defined, nonmodality-specific "durational" factor important to the solution of "sequential" tasks.

The manner in which the mediobasal forebrain structures, which, as we have seen, are characterized by "nonspecific" inputs, affect such a durational factor has been suggested elsewhere (Pribram, in press, b). Essentially, the telencephalon, as well as the diencephalon and mesencephalon, shows a gradient of organization from the ependymal lining outward. This gradient is expressed as the complexity of possible neuronal patterning within a system at any one moment in time. The mediobasal limbic systems of the telencephalon not only are heavily interconnected with the medial diencephalon and mesencephalon but also show functional similarities to these latter systems. Specifically, diffuseness rather than spatial or modality specificity characterizes the relationships of the mediobasal systems and peripheral structures. Activity in the mediobasal systems affects other central neural mechanisms through parallel connections so arranged that different amounts of synaptic delay are interposed in each of the connecting tracts: the result, cumulation of neuronal activity effecting changes of *excitability* of neural tissue, not changes in *momentary* patterns of activity. These changes in excitability are akin to electrotonic, synaptic, and dendritic potential changes rather than to the propagated nerve impulse. Thus, experiments such as the neuropharmacological ones dealing with neural phenomena showing a slow time course may in the immediate future be expected to increase our understanding of the behavioral processes affected by mediobasal system ablations and stimulations: i.e. behaviors categorized as feeding, fleeing, fighting, mating, and maternal.

SUMMARY AND CONCLUSIONS

We have traced the differentiation of the forebrain in nonmammalian vertebrates and detailed some of the constancies in the still more complex differentiation in mammals. We have seen that an attempt to correlate the progressive differentiation of the vertebrate forebrain with a progressive differentiation of the total repertoire of behavior patterns fails to find support in comparative psychological data; on the other hand, one aspect of behavior, i.e. the increasing capacity to make any particular response subject to multiple "sensory" and "motivational" determination, does appear to correlate with the increasing differentiation of the vertebrate forebrain. Contrary to earlier generalizations, which were based on the erroneous assumption that archi- and paleopallial structures were primarily devoted to olfactory processes, current available data are more harmoniously systematized by taking into account the progressive development of these medial and basal forebrain structures as well as the dorsolateral derivatives of the general cortex. The tentative formulation that the medial and basal forebrain structures partake in the increasing evolutionary differentiation of the forebrain finds support in the analysis of mammalian thalamocortical comparative morphology. An internal core of dorsal thalamic nuclei and their projections to the fronto-mediobasal aspects of the telencephalon can be distinguished in all mammals from an external portion of the dorsal thalamus and its projections to the postero-dorsolateral aspect of the telencephalon. The projections of the internal core of nuclei are intimately related to the archi- and paleopallial portions of the forebrain—significantly, however, newer formations such as the medial nucleus and its projection to the anterofrontal cortex develop within this internal core. Thus the classical dichotomy between older forebrain structures and new formations is modified for the purposes of our analysis: a dichotomy more relevant to this discussion is one between an internal or centrally located core of neural systems and an external portion of the forebrain. Each of these portions, the external and the internal, contains both old *and* new formations.

Each of the two major divisions of the forebrain is characterized by its input and by its functions in behavior. The external portion receives a sensory mode-specific input through tracts made up of large, long nerve fibers. These tracts are so constituted as to maintain a topological correspondence between the organization of receptor events and those occurring in the forebrain. The functions of the external portion in behavior have to do with the performance of discrimination tasks. Mode specificity and "differentiation" of cues are involved not only when those sectors which receive the input are studied but also when behavior is affected by manipulations of the "intrinsic" sectors of this external portion.

The internal core of the forebrain receives a nonspecific input through systems made up of fine, short nerve fibers diffusely connected by many synapses. These systems are so constituted as to influence the fluctuating excitability of the forebrain rather than to transmit patterns of signals. The functions of this internal core of systems in behavior have to do with the performance of tasks involving sequential response dependencies for their solution. Changes in the order and duration of the units constituting such a behavior sequence are involved not only when those sectors which receive the input are studied but also when behavior is affected by manipulations of the "intrinsic" sector of this internal core.

This formulation of the data of comparative neurology and comparative psychology proposes the following questions: Have we, in emphasizing the dichotomy between those formations which are represented in most vertebrates and those which are the special acquisition of primates, missed the significance of the equally important findings that in some form or another *all* forebrain structures are represented in all but the most primitive vertebrates; that differentiation does not take place in a "straight line" fashion, but that amphibia show a preponderance of paleopallial formations, reptiles and birds of archistriatal and archipallial structures, while mammals specialize in dorsal thalamus, neostriatum, and general (neo) cortex? Have we, in our preoccupation with the dichotomy between those formations which differentiate in presumably "lower" forms and those which differentiate in primates, lost sight of a distinction in forebrain anatomy which can be discerned in practically all vertebrates and dominates the picture in mammals: viz. the distinction between a core of internally situated forebrain formations and more externally placed systems? Have we, in emphasizing the dichotomy between behavior which is apparently determined by "innate" mechanisms and that which is apparently "learned," confused this dichotomy with an even more interesting distinction between behavior which is inflexibly determined and that which has multiple determination? Have we, in emphasizing the biological aspects of the "motivational" and the environmental aspects of the "sensory" process, missed the taxonomic significance of the difference between behavior involving the sequential dependency of responses and behavior involving discrimination? These are specific questions which can be answered by specific series of experiments and observations. Comparative neurology has a wealth of detailed knowledge which, if sifted with precision, care, and imagination, can form the foundation for hypotheses concerning the taxonomic behavioral schemes so basic to an understanding of the evolution of behavior. There *is* a place in our current scientific endeavors for such a comparative neurology:

> During the past half-century, morphology has seemed to be declining in favor, its problems submerged in the more attractive programs of the experimentalists. Nevertheless, activity in this field has not abated, and now there is a renaissance, the reasons for which are plain. Conventional methods of anatomical research have laid a secure factual foundation, but the superstructure must be designed on radically different lines. Several centuries of diligent inquiry by numerous competent workers have produced a vast amount of published research on the anatomy and physiology of the nervous systems of lower vertebrates; but most of this literature is meaningless to the student of the human nervous system, and, as mentioned at the beginning of this book, its significance for human neurology has until recently seemed hardly commensurate with the great labor expended upon it. The last two decades have inaugurated a radical change, in which we recognize two factors.

In the first place, technical improvements in the instrumentation and methods of attack have opened new fields of inquiry hitherto inaccessible. To cite only a few illustrations, new methods for the study of microchemistry and the physical chemistry of living substance, radical improvement in the optical efficiency of the compound microscope, the invention of the electron microscope, and the application of the oscillograph to the study of the electrophysiology of nervous tissue are opening new vistas in neurology, which involve quite as radical a revolution as that experienced a few centuries earlier when microscopy was first employed in biological research.

A second and even more significant revolution is in process in the mental attitudes of the workers themselves toward their problems and toward one another. A healthy skepticism regarding all traditional dogmas is liberating our minds and encouraging radical innovations in both methodology and interpretation. And, perhaps as a result of this, the traditional isolationism and compartition of the several academic disciplines is breaking down. The specialists are now converging their efforts upon the same workbench, and cooperative research by anatomists, physiologists, chemists, psychologists, clinical neurologists, psychiatrists, and pathologists yields results hitherto unattainable. What is actually going on in the brain during normal and disordered activity is slowly coming to light.

Here the comparative method comes to full fruition, and comparative morphology acquires meaning, not as an esoteric discipline dealing with abstractions but as an integral and indispensable component of the primary task of science—to understand nature and its processes and to learn how to adjust our own lives in harmony with natural things and events, including our own and our neighbors' motivations and satisfactions (Herrick, 1948).

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