THE BRAIN AND BEHAVIOR*

PSYCHOLOGISTS, because of their interest in developing ways of explaining and predicting human behavior, find it necessary to understand the physical and physiological characteristics of human beings. Any scientific analysis of behavior must take into consideration the structural factors or mechanisms which might be involved in the relation between environmental conditions and behavior. A psychology developed in ancient times, or in other parts of the world, might have directed its attention to the heart and the circulatory system or to the diaphragm and the respiratory or "pneumatic" system (Magoun, 1958; Veith, 1958; Woollam, 1958), but psychologists in Europe and America during the past hundred years have been concerned with the central nervous system as the relevant physiological mediator between environment and behavior. The purpose of this paper is to describe the neurophysiological model current around 1900 which was proposed as such a mediating mechanism and to contrast the simple, machine-like conception it involved with the complex model which more recent neurophysiological work requires.

Neurophysiologists are in agreement in dating the beginning of the modern period of research on the central nervous system to the observation in 1870 by two German neurosurgeons, Fritsch and Hitzig (1870), that an electrical current applied to the surface of a dog's cortex resulted in movements of the legs on the opposite side of the body (cf. Ferrier, 1886, p. 223; Penfield & Rasmussen, 1950, p. 12; von Bonin, 1950, p. 11; Konorski, 1958, p. 1102). The effect of

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their experiments which provided a new direction for research has been described by Konorski (1958) as follows: "From that time onwards, in almost all countries, but especially in Germany and England, various fields of the cortex were intensively explored with the aid of two methods: stimulation of various points of the exposed cortex in an anaesthetized animal, and testing of the results of ablation of particular areas after the animal has awakened from anaesthesia. The investigations were so numerous and rich in results that by the turn of the century, the chart of the function of the cortex of animals (rabbits, cats, dogs, monkeys and apes) was essentially completed, and, what is more surprising, it has proved to be not very different from that worked out more recently with the aid of infinitely more perfect methods. The investigations demonstrated that the cortex comprises the so-called projective (sensory) areas representing a cortical counterpart of particular receptor surfaces, the motor area, involved in voluntary movements of particular parts of the body, and areas of undefined function, which expand with the phylogenetic development of the brain and which were most frequently referred to as associative areas. As a rule, the results of the investigations were in conformity with the results of respective histological studies.

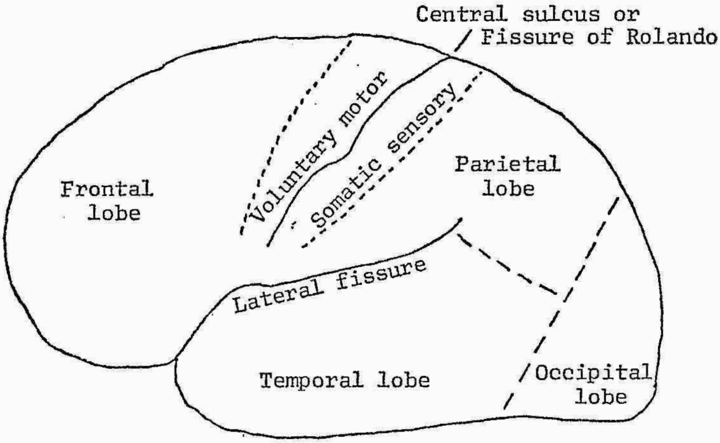
"However, it is interesting to note that after this general scientific assault, when all the positions susceptible to conquest with the aid of the methods then available had been tackled, development along this line suddenly came to an end. It seemed that after the functional topography of the cerebral cortex had been mapped out, there was nothing more left to be done in the physiology of the brain" (Konorski, 1958, pp. 1102-1103).

Konorski's remarks characterize the situation in neurophysiology at the turn of the century. An impressive amount of work had been accomplished; at that time von Monakow (1902) could review 846 references representing research conducted to explore the significance of Fritsch & Hitzig's original experiment. As a result of this research, neurophysiologists of 1900, as Konorski indicated, distinguished three major kinds of cortical areas: (1) sensory areas, which were connected by nerve fibers to the various sensory receptors in the body; (2) motor areas, which were connected by nerve fibers to the muscles; and (3) association areas, which did not respond to stimulation and which were believed to connect sensory with motor areas. The neurophysiological model linking environment to behavior could accordingly be described as follows: external physical stimuli impinging on the sensory receptors set up nerve impulses which were transmitted to sensory areas in the brain where they gave rise to sensations and perceptual experiences; from those areas nerve impulses passed through the association areas which were considered responsible for intellectual and emotional activities; and from there the impulses passed on to the motor areas with a resulting ennervation of muscle fibers and thus movements of the body. The significance of this model for the work of Pavlov, Watson, Hull, and others of the "Behaviorist school" of psychology is, of course, well known. Such a model provides a mechanical conception of human behavior with the brain as a kind of telephone switchboard connecting stimuli with responses.

Research in neurophysiology since 1900 has made it increasingly difficult to accept this simple interpretation of the function of the central nervous system. In the following sections of this paper selected examples of this more recent research will be described to indicate the kinds of neurophysiological data that contemporary psychology now has available to aid in the development of ways of explaining and predicting behavior. For the purposes of this presentation it is useful to divide the material into three sections, covering research dealing, respectively, with somatic sensory and motor processes, with intellectual processes, and with emotional processes.

SOMATIC SENSORY AND MOTOR PROCESSES

Before describing the research on somatic sensory and motor processes following Fritsch & Hitzig's discovery, it will be necessary to describe briefly some of the gross anatomical characteristics of the human cerebral cortex. Four major regions or lobes are usually distinguished for each cerebral hemisphere as indicated in the accompanying diagram, although the anatomical boundaries between each area are not in all cases clearly specifiable. The frontal lobe includes that portion of the brain anterior to the central sulcus or fissure of Rolando and superior to the lateral fissure. The parietal lobe extends from the central sulcus posteriorly and is



Side view of the human cerebral cortex

bounded by the lateral fissure. The temporal lobe is marked off by the lateral fissure and extends laterally and ventrally. The occipital lobe is located at the rear of the cerebrum, but is not separated by any major fissures. (For the purposes of this paper it will be appropriate to consider cortical areas in animals as comparable to those described here for the human cortex.)

The work that had been done by 1900 placed the cortical representation or projection of somatic sensory processes in the parietal lobes in a narrow region adjacent to the central sulcus. The motor processes were localized in the frontal lobes just anterior to the central sulcus. Along each of these narrow strips it was possible to identify topographical representations of the body for both sensory and motor processes beginning at the top of the hemisphere and extending down the side in the following order: foot, leg, trunk, neck, arm, hand, face, and throat (Ferrier, 1886, Ch. VIII; Sherrington, 1906, Lecture VIII). More recent work using more refined techniques has substantiated these early finding (cf. Penfield & Rasmussen, 1950, pp. 213-216), but has made it necessary to change the interpretation of their significance. In order to be able to clarify this change in interpretation it will prove helpful to describe in some detail the procedures involved in systematic electrical stimulations of the human cortex during operations on the brain.

Penfield and his colleagues (Penfield & Rasmussen, 1950; Penfield & Jasper, 1954) have performed more than four hundred operations on the human brain for the removal of tumors or other sources of epileptic disturbance. In order to insure the excision of all the diseased tissue it is necessary to identify precisely the limits of the pathological area. At the same time precautions must be taken to minimize interfering with those areas of the cortex which are essential for normal body function. Thus electrical stimulation of the cortex has a practical relevance for the treatment of the patient undergoing surgery. For the neurosurgeon the value of the results of this stimulation for establishing neurophysiological generalizations is secondary. Nevertheless, over the years Penfield and his colleagues have collected sufficient data from cortical mappings to be able to describe certain characteristics of the surface of the cortex in considerable detail.

The actual stimulation procedure is comparatively simple once the surface of the brain has been exposed. An electrode providing a brief current (a fraction of a millisecond) at voltages from ½ to 5 volts is touched to some point on the surface of the right hemisphere of the cortex. The patient, who is conscious throughout the operation, may report a tingling sensation on the upper portion of the left leg, flex the left hand, or perhaps contract the left leg. The location of each response is marked with a numbered ticket; a secretary records the numbers and the responses, and the total surface area with tickets affixed is photographed. After the excision of the pathological tissue, further stimulation may be carried out. Then the incision is closed. (Cf. Penfield & Rasmussen, 1950, pp. 4-9.)

As indicated above, the cortical diagrams Penfield and his associates prepared using all the apparatus available to modern neurosurgery were in substantial agreement with the diagrams prepared from studies of animals before 1900. But in the course of their work and the work of other neurophysiologists it became more and more difficult to understand the function performed by the sensory and motor projection areas in the mediation of environment and behavior. These difficulties arose in the course of investigations designed for three different purposes: (1) to specify more precisely the actual cortical points of stimulation and their effects, (2) to examine more closely the sensory and motor processes related to electrical stimulation, and (3) to determine the effects on behavior resulting from the surgical excision of cortical tissue.

(1) Attempts to specify more precisely the cortical points of stimulation and their effects ran into two kinds of difficulties. First, repeated stimulation of the same location for a particular patient did not always elicit the same response. Depending on other conditions, not all well understood, the stimulation of a point which had resulted in a particular response might yield the opposite response, a response appropriate to an adjacent area, a combination of several responses, or no response at all. Second, although the topographical mappings from patient to patient showed the same general order, the cortical location and the amount of tissue involved varied widely. For surgical purposes it was necessary to replot the effects of electrical stimulation for each patient (Penfield & Rasmussen, 1950). Not only were the responses to stimulation variable, but the tissues themselves varied greatly. Detailed histological studies of the cortex measuring surface, volume, thickness, number of neurons, and density, among other characteristics, reveal such variability between specimens that statistical analyses are coming to be accepted as necessary procedures (Lashley & Clark, 1946; Sholl, 1956). Lashley (Jeffress, 1951) found that animals grossly indistinguishable in behavior might have brains which differed by 100 per cent in the average size of cells in certain sections of the frontal lobes or by 50 per cent in the number of nerve cells in the temporal lobes; certain cells present in one brain might be absent in the other. Lashley concluded that "the anatomic variability is so great as to preclude . . . any theory

which assumes regularity and precision of anatomic arrangement" (Jeffress, 1951, p. 70).

(2) The studies designed to examine the sensory and motor processes relating to cortical stimulation were primarily concerned with the kinds of sensations and movements elicited. Penfield's observations are particularly pertinent in this context: "The sensation elicited was described as tingling, as sense of movement when no movement could be observed, and on the negative side as numbness. The words 'pain,' 'cold,' and 'blood rushing,' which may mean heat, were used only occasionally. Apparently no patient found it disagreeable. No forced reactions appeared as after painful stimulation. These are elements of sensation which do not carry with them specific memories. The patient knew accurately only where the sensation semed to be. He never suggestd that something rough or smooth or warm or cold had actually touched the part, nor did he believe that someone was moving the part" (Penfield & Rasmussen, 1950, pp. 216-217).

"Some of the movements are crude, others complicated, but they are all elementary. Thus, the movements of the contralateral leg and arm are those of simple flexion or extension. The hand opens or closes; no more. In the lower portion of the sensorimotor strip, however, stimulation may produce the following coordinated acts, which are not restricted to contralateral parts but are bilateral: (1) vocalization, a coordinated act carried out by skillful activation of mouth, pharynx, larynx, diaphragm, and abdominal musculature; (2) mouth movements as though eating or sucking, associated with salivation and swallowing; (3) turning to one side with conjugate deviation of the two eyes. The baby is able to do all of these things at birth, or not long afterward. But there is, in all of this, none of the acquired skillful foot movements of the dancer, nor any of the manifold delicate performances of which the adult fingers are capable. The mouth is never used to form a word" (Penfield & Rasmussen, 1950, p. 217).

It should be obvious from the quotations that although cortical stimulation of the sensory and motor areas produces effects which may be described as sensory or motor, these effects are so simple and so specific that they bear little relation to skilled behavior patterns or complex sensory discriminations. In further cortical explorations Penfield has found some evidence for secondary or even supplementary sensory and motor areas which seem related to more complex behavior patterns for the mouth and hand. However, the effects of stimulation in these areas can be noted only if the region stimulated is already active. Penfield's tentative conclusion is that, although the sensory and motor areas in the cortex may be way stations in the development of complex behavior patterns, they are clearly neither terminals nor points of origin.

(3) Another group of studies explored the effect on behavior resulting from the removal of tissue in the sensory and motor areas. The research on animals has been designed to determine the consequences of destroying individual nerve cells and fibers and of removing larger amounts of tissue. Lashley (1958) reports that more than one thousand cuts have been made in the cortex of the monkey without any discoverable changes in its behavior. In other studies knife cuts have been made in criss-cross patterns across the sensory and motor areas of a monkey's cortex and deep into the white matter of the hemisphere producing not only cell destruction but also severing the connections between cells; again, little or no defects have been reported in learning or the retention of habits (Sperry, 1958). The removal of larger amounts of tissue has been shown to have an effect on an animal's behavior. In Lashley's (1929) work on maze learning

in rats, he found a decrease in their efficiency proportional to the total amount of tissue removed. His experiments failed to demonstrate special significance for any particular area of the cortex. The results of removing cortical tissue from apes and humans, however, can not be understood in terms of this simple quantitative rule.

Operations on the primate sensory or motor areas result initially in some form of sensory deficit or paralysis. Penfield & Rasmussen (1950) report that the removal of the whole sensory projection area from one hemisphere of the cortex results in the loss of the sense of movement and of position in space of the arm and leg on the opposite side. Evidence documenting anesthesia for the area is contradictory, but it is clear that there is no permanent loss of the appreciation of touch, pain, or pressure. Total removal of the motor area in one hemisphere results in complete paralysis of the arm and leg on the other side, which may be accompanied by spasticity of those limbs. However, in a comparatively short time some movement is again possible, and, although the process of recovery is slow, virtually complete use of the limbs has been reported for some patients in less than a year. In other cases recovery never seems to be complete.

Franz (1929) reports that recovery from surgically induced paralyses in monkeys usually takes nine to twelve months. Using systematic exercising techniques coupled with immobilization of the unaffected limbs, he found recovery was substantially complete within thirty days. Application of similar exercising procedures to human subjects with paralyses of four or more years duration yielded similar results. Patients whose arms and legs had been useless became able to use them well enough for running, playing baseball, or sewing. In another kind of experiment Jacobsen (1934) removed the part of the motor area involving the forelimbs in chimpanzees who had been trained to open problem boxes with those limbs. Even though movement was curtailed by a severe temporary paralysis, the monkeys used their feet to help their arms open the boxes. The results of these and other studies involving tissue destruction or removal in the sensory and motor areas increase our uncertainty about the functions performed by those areas.

The recent neurophysiological research on somatic sensory and motor processes discussed in this section does substantiate the presence of specific areas in the cortex which when stimulated result in sensations or motor movements just as neurophysiologists in 1900 had claimed. However, studies designed to clarify the significance of these areas for the way the central nervous system mediates between environment and behavior preclude the acceptance of any simple, mechanical model. There is too much variability in response to stimulation for one subject, in cortical location and amount of tissue for a particular part of the body in different subjects, and in anatomical and histological characteristics. The kinds of sensory and motor processes which result from stimulation are crude and stereotyped; their relation to complex behavior sequences or sensory discriminations is obscure. The effects of tissue removal in the sensory and motor areas are variable and often only temporary. The available neurophysiological data require a much more complicated model for the explanation of the sensory and motor aspects of behavior than the one available to psychologists at the beginning of this century.

INTELLECTUAL PROCESSES

The technique of electrical stimulation introduced by Fritsch & Hitzig left more than half of the cortex unidentified (Ferrier, 1886, Ch. VIII; Sherrington, 1906, Lecture VIII;

Franz, 1907, p. 12). As indicated above, these portions of the cortex were called association areas because they were believed to connect sensory with motor areas. For various reasons the frontal lobes were singled out as the most probable locus for intellectual processes. Data from comparative anatomy identified this region of the brain as the last to develop in mammals and as most highly developed in man (Ferrier, 1886, p. 466; Ariëns Kappers, Huber & Clark, 1936, Ch. X). In addition a number of clinical studies of brain tumors or traumatic lesions in human frontal lobes gathered during the 19th century reported intellectual deficits, although as Franz (1907, Ch. II) has indicated, there were an equal number of cases in which no deficit was reported. In spite of this equivocality Ferrier (1886) felt justified in stating, "We have . . . many grounds for believing that the frontal lobes . . . form the substrata of those psychical processes which lie at the foundation of the higher intellectual operations" (p. 467). However adequate or inadequate the initial grounds might have been, a large amount of research has been undertaken to explore the significance of the frontal lobes for intellectual processes.

The problems involved in demonstrating the relation of the frontal lobes to intellectual processes were more difficult than those encountered in exploring the significance of the sensory and motor areas of the cortex. In the latter case, electrical stimulation of the tissue had a definite effect, although, as recent research has demonstrated, the relevance of these effects for the function of the central nervous system is not yet clear. However, with the exception of the somatic motor area, stimulation of the frontal lobes had no effect and the neurophysiologist had to vary systematically both his cortical procedures and his behavioral measures. As a consequence research on this problem has been controversial from the start.

The earliest studies on animal behavior involving surgical removal of frontal lobe tissues were done without clear-cut anatomical or behavioral criteria for evaluation of the results. Bianchi's (1895) work on monkeys and dogs is typical. The location and amount of tissue to be removed was essentially uncontrolled, varying from animal to animal. It was therefore difficult to compare the results from different operations. The only data on the effects of the surgical procedures were in the form of anecodotal reports of changes in behavior or "psychical condition" manifested in the laboratory setting. Again it was impossible to compare the results from subject to subject. Bianchi, working with these limitations, concluded that operations on the frontal lobes did influence the intellectual functions of his animals. Others working at the same time with similar limitations arrived at the opposite conclusion (cf. Horsley & Schäfer, 1888).

Beginning about 1900, Franz (1907) began a series of studies on monkeys and cats designed to specify more precisely the cortical lesions produced and to measure the effects of the operations on specific habits. He trained the animals to open puzzle boxes; then, after systematically varying the amount and location of cortical tissue removed for different animals, he tested them again on the original problems. Although the results were not wholly consistent, Franz felt that his data warranted the conclusion that destruction of tissue in the frontal lobes results in the loss of the newly formed habits which, however, could be relearned. Well established habits were not affected by the operations.

Subsequent studies have varied both the lesions and the kinds of tasks required of the animal. Lashley's (1929) work on the performance of rats in mazes cited above led him to favor a quantitative hypothesis: the amount of tissue removed is relevant, but not its location. Jacobsen's (1931) studies on the performance of monkeys on a variety of tasks led him to conclude that lesions in the frontal and prefrontal areas had no effect on either retention or learning of simple problem-box or pattern discrimination habits. Some impairment was noted in the retention of a more complex combination-box habit, but this effect was also noted in parietal lesions so it could not be attributed to the frontal lobes themselves. In a later study Jacobsen (1935) found that bilateral removal of the frontal lobes affected the performance of monkeys on tests which required temporal sequences of movements or delayed reactions. The interpretation of Jacobsen's later work and of the volume of research since that date is still a subject for controversy (cf. Fulton, 1951, pp. 92-94). It does seem to be justifiable, however, to offer the tentative conclusion that, if the frontal lobes are significant for intellectual processes in animals, they are necessary only for complex behavior patterns.

The data on the effects of tissue removal from the human frontal lobes are, of course, far less systematic and carefully controlled than the data from animal studies. The evidence available comes primarily from observations of the results of surgical operations conducted for two different kinds of reasons. (1) Tissue from the frontal lobes has been removed because of the presence of tumors or traumatic injuries in those areas. (2) Surgical intervention in the form of tissue removal or the section of nerve fibers has been performed for psychiatric purposes. A discussion of the rationale underlying the use of surgical procedures for psychiatric purposes will be deferred until the consideration of emotional processes in the next section.

(1) Many of the clinical reports describing the effects of frontal lobe operations performed to remove tumors are poorly documented. Cases reporting gross defects of behavior

alternate in the literature with those which fail to record any behavioral changes. The clinical value of the operation for the particular patient usually has determined the kinds of observations that were made, and few, if any, kinds of controls or systematic comparisons have been used to evaluate the conclusions. (Cf. Franz, 1907, pp. 16-24; Hebb, 1945; Sholl, 1956, pp. 73-76.) Even more carefully designed studies could not be accepted without reservation. Rylander (1939a, 1939b) used a comprehensive battery of tests in his study; besides intelligence tests, he had techniques designed to measure, among other things, attention, memory, the ability to abstract common characteristics from a set of objects, and the formation and use of abstract ideas. For each patient a "normal" control subject was chosen of the same age, sex, education, occupation, and social background. Rylander found changes in test performance for twenty-one of his thirty-two patients. On the basis of his data he concluded that the surgical removal of tissue from the frontal lobes causes intellectual deficit. A re-evaluation of the studies of Rylander and others by Hebb (1945) makes it impossible to accept this conclusion.

Hebb (1945) prepared a critical view of neurosurgical reports on the functions of the frontal lobes as a result of his observations on a patient who had had both frontal lobes removed. The operation was done to correct epileptic attacks attributed to a skull fracture some ten years before which as it turned out had destroyed both frontal poles. Before the operation the man was childish, violent, stubborn, and destructive; afterwards it was impossible to demonstrate psychological defects. All of the effects of the removal of a large portion of his frontal lobes seemed to be positive. Intelligence test scores indicated that his IQ had changed from 70 to 96, this last index well within the normal range. Social adjustment and intellectual performance after the operation were such that, in spite of careful medical and psychiatric screening, the patient was accepted by the army and spent ten months overseas before an epileptic attack, apparently brought on by hard labor, resulted in his discharge. Hebb was disturbed by the absence of gross defect in this patient in contrast to the reports from other cases which involved similar operations, so he made a careful analysis of such studies.

Pared to its essentials, Hebb's critique may be stated simply. Previous studies reporting extreme behavioral deficit had drawn their conclusions on the basis of a common logical paradigm. They had removed tissue from the frontal lobes *and* changes in behavior had been observed; therefore, they argued that the tissue removal had caused the changes in behavior. This logical device of *post hoc ergo propter hoc* is fallacious, and Hebb hastened to point it out. Simple succession in time is not sufficient to establish causal relations. A more detailed description of the operation and the context in which it was performed will clarify the problems Hebb found in interpreting previous results: (a) Prior to the operation the patient was hospitalized for some neurological disorder which may have had a history of many years duration. (b) Immediately before the operation the patient's behavior was observed and studies were made of his performance on certain tests. (c) During the operation, incisions were made in the brain, and certain amounts of tissue were removed. (d) After the operation, the patient's behavior was observed, and studies were made of his performance on certain tests. It seemed to Hebb that for each of these four conditions influences were present which made it impossible to attribute changes in behavior solely to tissue removal.

(a) The previous history of the patient must be considered.

The length of his illness and the degree to which it has affected his normal activities, his job, and his financial status are relevant variables. The effect of the illness on his family and their attitude toward him and his operation may be pertinent. Finally, the patient's conception of his illness and of the possible consequences of the operation also enter in. The neurological disorder is not the only factor influencing his behavior prior to the operation.

(b) Observations of behavior and tests of performance for one subject must be interpreted cautiously. No measure of intellectual functioning is perfectly reliable; judgments of test reliability can only be made for groups of subjects. In addition, the conditions listed under (a) certainly make it difficult to conclude that the pre-operative performance reflects the typical behavior of the patient.

(c) The operation itself also provides sources of variability other than tissue removal. It is difficult to determine whether all the defective tissue has been excised. Even where that seems to have been accomplished, scarring and subsequent atrophic changes might occur. Tumor growths have been found to cause pathological changes at some distance from their locus because of compression. In addition, it is necessary to realize the possible effects of the operation on blood supply, chemical changes in the cells, and the like.

(d) The interpretation of the changes in behavior and test performance after the operation are subject to the same qualifications noted under (b). Variability in performance by a subject on successive testings is expected; this variability can only be evaluated if the patient population is sufficiently large for statistical tests of significance. After the operation the patient is aware that certain portions of his brain have been removed and his conception of their significance will undoubtedly influence his behavior. Moreover, his status as a patient has changed, both for himself and for his family, e.g., whether he would be able to return to his normal activities after discharge from the hospital.

The factors described under these four headings make it apparent that an intellectual deficit, if present, can not be attributed solely to surgical removal of tissues from the frontal lobes as Rylander had claimed. No matter how carefully the tests have been selected or how comprehensively they sample the relevant behaviors, any changes in test performance reflect changes in the patient's total situation. Although the use of a control group is certainly pertinent for studies of this kind, it is at present impossible to know what factors need to be controlled. Age and amount of education can be equated, but hospitalization for a year and failure to earn an income for that period of time may also need to be considered. Other studies could be cited in elaboration or extension of these considerations, but Hebb's conclusions seem unavoidable: "no one has as yet shown that defects follow a simple loss of tissue from man's frontal lobes." He does go on to say, "the loss must, presumably, have some effect, but it is hard to demonstrate and its nature is not yet clear" (Hebb, 1945, p. 24).

(2) Systematic studies of operations made on the frontal lobes for the therapeutic treatment of psychiatric patients support Hebb's conclusions about our knowledge of the role played by the frontal lobes in intellectual functions. For the present purposes it will be sufficient to describe briefly the results of two of the most carefully controlled studies: the Columbia-Greystone Project (Mettler, 1949) and the Second Lobotomy Project of the Boston Psychopathic Hospital (Greenblatt & Solomon, 1953).

The Columbia-Greystone Project (Mettler, 1949) was designed to permit a systematic evaluation—medical, psychological, psychiatric—of the results of bilateral symmetrical removals of tissue in different anatomical areas of the frontal lobes. None of the patients showed any permanent impairment of function from the operation which could be demonstrated on an extensive battery of psychological tests. No loss in memory, learning, or intellectual functions could be attributed to the operations; instead, gains in recall and recognition scores were often observed. Impairment of the ability to abstract or generalize could not be regularly demonstrated. No permanent changes were noted in intelligence test scores; transient losses were usually regained within four months. The overall evaluation of the Columbia-Greystone Associates is that the frontal lobes do not seem to play an important role in intellectual functioning of the kind required for the tests they used.

The lobotomy operation performed in the Boston Psychopathic Hospital studies (Greenblatt & Solomon, 1953) does not involve removal of tissue from the frontal lobes. Instead, small holes are bored in the top or side of the head and a knife used to sever the fibers which connect the frontal lobes with other areas of the brain. Assessment of changes following the operation showed, if anything, improvement in intellectual functioning. Ability to think conceptually or abstractly and make inferences improved; thinking seemed more controlled and coherent. The changes certainly must be understood in relation to low test scores before the operation and to the psychiatric status of the patients which may have influenced those scores. However the improvements might be explained, it is clear that the operation did not reduce intellectual functioning in any way that the methods of assessment used in this study could identify.

The conclusions reached by Hebb and the staff of the two projects cited leaves the role of the frontal lobes in intellectual processes highly uncertain. More work is being done; some investigators have studied the effects of frontal lobe lesions in relation to other ways of measuring intelligence, biological intelligence for example (cf. Halstead, 1947), but most neurophysiologists are concerned with exploring the neurophysiology of intellectual processes in different kinds of ways. A quotation from Lashley seems appropriate at this point. He says: "In fantasy, I have thought perhaps that my most important contribution when I reach retirement age would be to have my frontal lobes removed and see what I could do without them. I have less confidence than Dr. Halstead that it would preclude the production of something of interest" (Jeffress, 1951, p. 145).

EMOTIONAL PROCESSES

In 1900 the neurophysiologist's knowledge about emotional processes in relation to the functions of the cerebral cortex was in some ways comparable to his knowledge of the cortical components of the intellectual processes. Electrical stimulation of the cortex had failed to elicit emotional responses just as it had failed to produce responses which could be identified as intellectual. So studies of emotional processes also began by removing various parts of the association areas and observing behavior subsequent to the operation. However, the emotions in contrast to the "higher intellectual operations" were never considered distinctively human; if anything, they were a part of man's animal nature and, as such, the cortical regions which developed latest phylogenetically were not necessarily involved.

Neurophysiologists studying emotions following Fritsch & Hitzig's discovery had less grounds for attributing a central role to the cortex than did those who were interested in intellectual processes. Experiments had been completed by

1886 so that Ferrier could report that "animals deprived of their cerebral hemispheres are still capable of exhibiting, in response to various forms of sensory stimulation special and general, reactions, more or less complex, which do not at all differ in character from those which we associate with feeling or emotion" (Ferrier, 1886, p. 146). He felt the evidence was sufficient to justify concluding that "the centres of emotional expression are therefore situated below the centres of conscious activity and ideation" (p. 147) which he considered to be located in the cerebral cortex. Ferrier did not specify clearly how he thought cortical mechanisms might be related to emotional expression. However, since emotions did affect states of consciousness, which for Ferrier were cortically determined, he felt that the activity of the centers of emotional expression must be represented in some form in the cortex.

Sherrington (1906) was more specific about his conception of the relations between the cerebral cortex and emotional processes. His studies of animals whose cerebral hemispheres had been removed led him to consider their emotional behavior as "pseudaffective," "mimetic movements simulating expression of certain affective states" (p. 251), but actually quite different from such states in the normal animal. In contrast to James and Lange who believed that emotions were reactions to visceral stimulation, Sherrington, representing the dominant tradition in neurophysiology at that time, argued that, although subcortical mechanisms were definitely involved, the initiation and maintenance of real (not "pseudaffective") emotional reactions were determined primarily by the cerebral hemispheres.

The identification of the frontal lobes as the areas of the cortex related to the emotions was suggested in early research by Bianchi (1895) and others, but the conception of the relationship was not clearly stated at that time. Bianchi reported that for his monkeys "friendliness and sociability (are) impaired; . . . their avidity becomes reckless and insatiable," and he spoke of "a dissolution of the psychical personality" (1895,p. 522). His results contrasted with the negative findings of Horsley & Schäfer (1888) just as they had for observations of intellectual processes. Franz (1907) in his more carefully controlled studies stated that "the emotional condition of the animal remains the same after as before the removal of the frontals" (p. 63). However, although Franz had systematic ways of evaluating the effects of the operations on habits, his judgments of emotional change were as anecdotal as those of his predecessors.

Much of the subsequent neurophysiological research on emotions is associated with the work of Cannon (1929) and Bard (1928, 1934a, 1934b, 1950). They began by studying more carefully the effects on animal behavior resulting from removal or isolation of the cerebral hemispheres. They observed in their animals a complex rage reaction elicited by trifling disturbances and distinctive for its intensity and breadth of expression. This "sham rage" was quite different from the "pseudaffective" reactions noted by Sherrington which were more similar to a normal animal's expressions of mild anger. Further research led them to identify the hypothalamus, one of the subcortical regions of the central nervous system, as the mechanism involved in the production of sham rage. Destruction of tissue which left the hypothalamus intact resulted in sham rage; direct stimulation of the hypothalamus produced the rage reaction; destruction of the hypothalamus eliminated it. Once the functions of the subcortical center for emotional expression were identified it became necessary to determine the way in which the cerebral cortex itself was involved in the process.

The studies of the hypothalamus suggested that the cortex acted as an inhibiting agent in emotional behavior. Since the hypothalamus was directly connected by nerve fibers with regions in the frontal lobes, subsequent research on emotional processes focused on the same cortical areas that had been involved in research on intellectual processes. Some experiments had reported that removal of certain portions of the frontal lobes did result in hyperexcitability for some animals. Bard's (1950) work on cats involving total removal of the frontal lobes failed to reveal changes in their emotional behavior. However, removal of most of the cortex except for certain portions of the frontal lobes resulted in an exaggerated placidity. When these frontal areas were removed in the placid animals, they displayed the characteristic sham rage reactions. Bard concluded that the frontal regions of the cat's brain "contribute equal excitatory and inhibitory effects" (1950, p. 217) in their influence on rage reactions. The particular manner in which these effects are accomplished is still being studied.

The significance of the research conducted by Cannon & Bard for understanding the function of the human frontal lobes is not clear. The stereotyped rage reactions characteristic of cats do not generalize readily to human behavior. Research on the effects of frontal lobe removal in primates seemed to contradict the findings of Cannon & Bard. Jacobsen (1931, 1935) reported that "no permanent emotional changes were found" (1931, p. 339) in his studies of monkeys which have already been discussed in connection with intellectual processes. His data did not permit him to decide whether the frontal lobes might have an inhibitory effect or whether some change in distractibility could be said to result from the operations. However, some of Jacobsen's monkeys did show a reduction in temper tantrums and anxiety behavior under frustrating conditions. When these results were reported at the Second International Neurological Congress in 1935 (Fulton & Jacobsen, 1935), they made a significant impression on Egas Moniz, a Portugese neurosurgeon, who felt that such an operation might be helpful for psychiatric patients. As a result Moniz (1936) developed the frontal lobotomy, a surgical procedure which involved severing the nerve fibers connecting the frontal lobes with the hypothalamus and other subcortical centers (cf. Fulton, 1951, pp. 98-100; Freeman & Watts, 1950, pp. xvi-xvii).

The theoretical considerations which Moniz advanced to justify this operation have been described as follows: "In the course of daily life . . . the human individual responds to various external happenings but in a very flexible manner. Certain happenings, however, serve to elicit responses that tend to become stereotyped, conditioned and thus indicate a certain stabilization of synaptic patterns in the nervous system. The stereotyped patterns of behavior on the part of mental patients seem to result from such stabilization, and shock methods are designed to break them up by forcible disruption of the synaptic connections. Prefrontal lobotomy has the same effect. By disrupting the stabilized synaptic patterns it abolishes the abnormal conditioned responses and restores the patient to a more flexible type of behavior" (Freeman & Watts, 1950, pp. 540-541).

Since 1935 when frontal lobotomies were first systematically performed for psychiatric purposes, tens of thousands of patients have been treated by that procedure or by variations which involved removing different amounts of frontal tissue from different locations (cf., e.g., Mettler, 1949; Freeman & Watts, 1950; Fulton, 1951; Greenblatt & Solomon, 1953). Moniz (1936) reported that an impressive number of his patients showed dramatic emotional changes: elimination of depression, relief from anxiety. With the increased use of lobotomy the results reported became more varied. Some patients were helped; for others serious disturbances followed the operation; for others no noticeable differences in behavior could be detected. At the present neurophysiologists, neurosurgeons, psychiatrists, and psychologists are by no means agreed about the appropriateness of the operation or the significance of its effects.

Freeman & Watts (1950) were among the first to perform frontal lobotomies in this country. Summarizing the results from studies of patients on whom they had operated over a thirteen year period, Freeman & Watts reported that about 45 per cent have shown good improvement, 33 per cent only fair, while 19 per cent did poorly. On the basis of their results they believe that the frontal lobes are concerned with the future, providing "foresight and insight" for the normal person. When the frontal lobes are damaged as in lobotomy, inertia, loss of self-consciousness, and lack of ambition result, and the patient's behavior may be characterized by euphoria, aggressiveness, and poor judgment. Freeman & Watts are convinced of the efficacy of the operation in psychiatric cases and believe that their results provide evidence about the functions of the frontal lobes in emotional processes.

Other studies of the effects of surgical procedures for psychiatric patients have been less confident about the value of the operation and its relevance for understanding the frontal lobes. Carney Landis, reporting for the Columbia-Greystone Project cited earlier, stated that "there is no clear-cut evidence of a consistent or uniform personality change which resulted from any particular variety of topectomy (removal of tissue from certain parts of the frontal lobes) in which the operation could clearly be said to be solely responsible for the change. The amelioration from psychosis and social improvement which occurred in many of the operatees is easiest understood as an indirect effect of the operation. If any operation specifically changed behavior some clear-cut regular phenomena should have been evoked. If any variety of operation had specifically resulted in the alleviation of some physical or mental disease or in the change of a particular personality structure, then greater regularity of results should have been achieved. It is an old clinical observation that any of a wide variety of physical injuries may be followed by a temporary amelioration of psychotic symptoms. Mentally disturbed patients are frequently relatively lucid during convalescence from an appendectomy, while recovering from a broken leg, or following an acute bout with an infectious disease. It is conceivable that the mental amelioration following topectomy might be basically the same sort of thing" (Mettler, 1949, pp. 494-5). In brief, as Landis went on to say, "No existing theory or hypothesis dealing with the psychologic significance of the human frontal lobes is tenable" (Mettler, 1949, p. 496).

Neurophysiologists in 1900 were less clear about their conception of the cortical mechanisms involved in emotional processes than they were about those related to sensory-motor and intellectual functions. As the studies cited in this section illustrate, it is not possible at this time either for neurophysiologists to specify unequivocally the function of the frontal lobes in emotional processes. Hypotheses have been advanced, but the data gathered to document them has not been sufficient to secure a consensus. Part of the difficulty in studies of emotional processes in contrast to those concerned with sensory-motor or intellectual activities can be attributed to the relative lack of clarity in specifications of emotional behavior. The use of lobotomies and lobectomies for psychiatric treatment represents a significant affirmation on the part of some neurosurgeons and psychiatrists of the adequacy of our knowledge of the central nervous system and its relations to behavior. They believe that some types of disturbance in a patient's life are serious enough to justify a radical procedure in spite of the inadequacy of our knowledge and because such operations might add to that knowledge. Others believe that until we understand more about the neurophysiological functions of the cortex such operations should not be performed. Further research will in time provide data which should allow this issue to be decided, providing that more adequate criteria for specifying emotional behavior are developed.

Discussion

In the preceding three sections selected studies have been examined which illustrate contemporary knowledge about the relations between certain parts of the cerebral cortex and somatic sensory and motor processes, intellectual processes, and emotional processes. While neurophysiologists in 1900 were confident about the adequacy of their understanding of the ways in which the brain functioned to mediate between the environment and behavior, neurophysiologists of the present are far from certain. Penfield & Rasmussen (1950), discussing the neurosurgeon's interest in the functions of the central nervous system, noted that "he must endeavor to determine what areas may be removed from the cerebral cortex without producing functional defects. His goal is achieved if he learns nothing at all positive about function! He thus discovers that removal of certain areas produces no defect that he or the patient recognizes. . . . The surprising fact is that so large a proportion of the human cerebral cortex may be called *dispensable cortex*" (p. 201).

Contemporary neurophysiologists, while uncertain, are far from inactive. Extensive research studies are being conducted, some along the lines of the research described above in attempts to specify more precisely those neurological variables, others exploring new kinds of variables, biochemical and electrical as well as physiological. Eccles, commenting on a paper which reviewed the "Early development of ideas relating the mind with the brain" (Magoun, 1958), remarked as follows: "Prof. Magoun has been very subtle in presenting us with his paper, because it shows how intimately our thinking is dependent upon what is known anatomically. It is a warning for us. Here we have seen the attempt to fit function to the crude anatomy which was all these physiologists had in those days; and they could only fit crude functional interpretations. Do we still err so remarkably? In some hundreds of years' time, will our present concepts look so archaic, simply because we are still fitting them to the only anatomy we have, which is what the anatomists give us? In the nervous system, we physiologists are more dependent upon what the anatomists tell us than we are anywhere else. Have we finally reached some of the basic levels of anatomy upon which we can securely build, e.g., the neurone, the synapse and all the more detailed material which is now coming with electron microscopy? Is this in turn to be superseded, and are we to look archaic? It is a very sobering thought" (Wolstenholme & O'Connor, 1958, p. 24).

Lashley's comments on the relations between brain and behavior viewed in the context of phylogenetic studies are also pertinent: "When comparing the brains and the behavior of animals at different levels in the phylogenetic scale, I have been much puzzled by the lack of significant correspondences. The brains of insect, cephalopod, bird, and mammal are as unlike in gross structure and arrangement as one can well imagine. Yet these animals show essentially the same fundamental types of behavior. They all learn, and with simple tasks and optimal conditions at about the same rate. They show the same types of perceptual generalization, the differentiation of figure from ground, the recognition of similarities among objects. All show similar perception of spatial relations. There are even suggestions of insight, or a primitive grasp of logical relations, by animals as primitive as the arthropods. The differences are quantitative rather than qualitative.

"It looks as though these basic mechanisms of behavior are somehow inherent in the structure of the nerve net, in the primitive organization of nerve cells, and are largely independent of the gross structures which have been evolved in phylogenetic history. Evolution of the nervous system seems to have been largely a matter of meeting the demands of the moment and of irreversibility of what has once been started. The primitive mammal was almost certainly nocturnal, making little use of vision. The cerebral hemispheres consequently developed as an outgrowth of the then dominant olfactory brain. Had the creature been diurnal, its intellectual development might have centered on the midbrain with enlargement of the optic lobes, but with no great difference in the final intellectual achievement.

"My point is that, although the detailed tracing of the structural changes of the brain in evolution is important for understanding of the evolution of the brain, the gross structural changes may be almost completely irrelevant to the problem of the evolution of behavioral or mental traits" (Association for Research in Nervous and Mental Disease, 1954, p. 95).

The statements of Eccles and Lashley present a broader perspective within which to view the research described in the previous sections of this paper. Considering that psychology is interested in data which would aid in the development of ways of explaining and predicting behavior, it might seem at first that current neurophysiological findings are of little value. Certainly, the neurophysiologists of 1900 provided a clear, simple, mechanical model which early psychologists could and did use to develop their theories. Contemporary neurophysiology does not provide such a model, but, by revealing the complexity and flexibility of man's structural characteristics, it forces psychology to develop richer and more refined ways of specifying both behavior and the conditions under which it occurs. Such a specification will be necessary for the development of neurophysiology itself, for as Harlow (1958) has pointed out and the material in this paper can illustrate: "no interdisciplinary research (in this area) can be better than the behavioral measures which provide its dependent variable or variables" (p. 5).

To the extent that Harlow's statement is relevant, it would seem that the differences in the results of research on sensory-motor, intellectual, and emotional processes noted in the preceding sections of this paper might be related to differences in the adequacy with which the behaviors involved for each can be specified. Observations of sensory and motor processes can be made both objective and measurable. Studies of intellectual processes are less objective, but it is still possible to specify criteria for their measurement. Judgments about emotional processes are neither objective nor measurable. To the writer it would thus appear that, following Harlow, the future of research on the relations between the brain and behavior would depend more on the adequacy with which we can refine our techniques for measuring behavioral variables and less on developments in neurophysiology, neuroanatomy, or biochemistry. Thus, although research in neurophysiology since 1900 has not resulted in a model for explaining and predicting human behavior, it has freed psychology from the necessity for working with simple, mechanical conceptions. At the same time, the responsibility of the psychologists for providing clearer and more rigorous specifications of behavior has increased. Both of these consequences should be beneficial to the development of psychology.

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