THE EFFECT OF BRAIN DAMAGE ON RAT INTELLIGENCE

by

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PREFACE

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HISTORICAL INTRODUCTION

The importance of the brain as the essential basis of intelligent behavior is taken for granted by modern psychology. Although no text-book would claim that even the principal relationships between brain function and intelligence have been adequately formulated, modern research assumes that a detailed and comprehensive account needs only time and continued effort for its ultimate appearance.

The conflicting views in the contemporary literature on the physiological basis of intelligence probably reflect differences of method - for example, what experimental subjects are used, - as well as differences in theoretical assumptions. The degree of divergence is illustrated by two recent publications. Halstead (1947), working with cases of removal of frontal lobe tissue in cases of brain tumor, concluded that this portion of the brain is essential to "biological intelligence": the frontal lobes are "the organs of civilization." But the Columbia-Greystone Associates (1949), working with cases in which frontal lobe tissue was removed to alleviate mental illness, found no evidence of permanent alteration in any intellectual function. Research on other parts of the cortex is in the same state, and gives no more immediate promise of showing us how intelligence is related to the brain. That it is dependent on the brain, we know; but how, what the details of the relationship are, we do not know.

A major source of difficulty is the obvious fact that radical experimentation is not possible with human subjects. In other such problems, as in understanding epilepsy, or genetic mechanisms, or gastric functions, real advances have often followed upon the successful application of animal experiment to the problem in hand. The necessary first step, of course, is to establish in an animal a homologue of the human phenomenon in which one is interested. Provided that there is a reasonable anatomical or functional similarity, one can then experiment freely with animals and later apply one's results to man. But in the study of intelligence we are faced with a special difficulty: the fact that intellectual function is the characteristic in which man and animal are most clearly different - so much so, that it may even be denied that animals and men have anything intellectually in common.

Moreover, research in physiological psychology has not done much to refute such an opinion. There has not been any great success in demonstrating parallel effects on intelligence in (a) experiments upon the animal brain and (b) the pathological "experiments of nature"plus the cautious operations of the neurosurgeon, in the human brain. In the animal field, Lashley's results (1929, 1935) are still generally accepted. Utilizing precise experimental controls, he systematically explored the effects of cortical injury on rat behavior. His general conclusion was that the efficiency of performance in complex activities is reduced solely in proportion

to the amount of brain injury: the principle of "mass action." On the other hand clinical studies not too infrequently report little or no change in a patient's intelligence after considerable brain damage. Although the fact of mass action has been repeatedly demonstrated in rat behavior (Morgan and Stellar, 1950), the principle is far from being accepted for man.

The suggestion has sometimes been made that the brains of rats and men are quite different. There may be more "encephalization" in man, or taking over by higher neural centers of functions which in lower animals are served by spinal cord and brain stem; and there may be a great increase in specificity of human cortical functions. Before agreeing with this approach, however, we may consider the possibility that the apparent differences are artifacts of method, and perhaps give more attention to the methodological problem of identifying phenomena in the rat which are analogous - or homologous - to human problem-solving.

Superficially, as we have seen, there may appear to be little in common in the intellectual activities of the two species. But some of the difficulty may reside in one's interpretation of that multivalent term, intelligence. The first step in an attempt to clarify the problem may be to review the background of the conception of intelligence in man and animal.

By the end of the 19th century, the implications of evolu-

tionary biology had begun to influence psychological thinking very markedly. Individual differences of ability and so on were stressed as a natural biological quality of organisms; the more "fit" variations of behavior, as well as of structure, tend to survive. Man's mind or his intelligence was by implication assumed to be his greatest biological asset. Natural selection had produced a higher mammalian intelligence, and one problem was how to measure it and possibly plan to produce even greater intelligence. Galton was able to show that eminence tended to run in families, and he founded eugenics in the attempt to improve the intelligence of the English "race."

In America, the leader in research in individual differences was Cattell. He concentrated on studying the range of individual differences in reaction time, association, attention, and so on. The battery of tests which he devised was intended to be expanded over the full range of human capacities, so as to comprehend fully the psychological nature of man. Cattell became particularly interested in being able to describe the situations that led to the development of men of scientific eminence.

Perhaps the more important feature of such interests was the growth of British statistics in response to the need for the organizing of the results of all the testing. The positive correlations between various tests led Spearman in 1904 to suggest that there was a common factor in these different performances. He called this general factor g, and workers began to assume that this was the general factor of intelligence.

But the tests were found to have no significant relation to scholastic success, which presumably reflected variations in individuals' intelligence. In working on this side of the problem - predicting academic achievement - it was Binet in France who made the significant contribution.

Binet had been made a member of a government commission concerned with the detection of retarded children by "pedagogical and medical examinations" for the special classes. He had made contributions in the field of mental testing (as it then stood) but he suspected that these tests were not getting at the "higher mental processes" which really constituted intelligence. The type of test that he believed was necessary was one which tested judgment, reasoning, comprehension, and so on. Instead of any elaborate laboratory apparatus as was often used in the earlier mental testing, the new intelligence test devised by Binet required only that the tester present short and easily administered questions and problems to the subject. The subject almost immediately "fails" or "passes" an item of the test (such as, "Name the months of the year" or "Which of these pictures is prettier?"). The problems were constructed so as not to be dependent on specific information that a child would obtain only from formal teaching, but were supposed to be such that the intelligent child with no schooling could solve them. By standardizing the test as a whole on groups of normal children, Binet was able to get a score for any particular child which was expressed as a "mental age": a mental age of 9 meaning roughly the ability to do as

well as the average nine-year-old. Another worker, Stern, suggested dividing the mental age by the chronological age to give a "mental quotient" to which Terman gave the now familiar name "intelligence quotient" or IQ. The success of the method was dramatic, and from it sprang the whole complex array of current intelligence tests.

These tests can be separated for the purposes of this discussion into two types: (1) the homogeneous mental tests which assess various human abilities or capacities separately, and which now include most of the types of item found in the Binet test, and (2) the general intelligence tests, which are still composite tests. The point for consideration is what these two types of tests indicate as to the nature of human intelligence.

If we were to adopt Spearman's approach to the general intelligence test, we would expect a good test to show that it was highly saturated with the general factor g. Statistical analysis of the Binet test, however, does not show a prominent general factor. It seems that the difficulty lies more in the Spearman technique rather than the construction of the Binet test. As Thurstone (1938) has shown, the analysis for g is only a special case of a more general kind of analysis. Intellectual capacity can be understood as composed of several independent factors. Working on this assumption, Thurstone has proceeded to build purified mental tests - tests which he considers as most clearly measuring factors in the intelligence-test performance. These separate tests are each highly saturated with one factor. This approach leads to the con-

ception of human intelligence as the sum of several, nearly independent, "primary mental abilities."

Thurstone, of course, does not wish to imply that his method has as yet uncovered all of the primary mental abilities in intelligence. If intelligence testing is to be satisfactorily organized in terms of testing separate mental abilities, then we should be interested first in finding out what the other primary abilities are, which compose the "impure residue" of the present general intelligence tests. The nature of some of the other possible factors in the general intelligence test has been discussed recently by Wechsler (1950).

Wechsler accuses Thurstone, perhaps unjustly, of limiting his work by concentrating only on the cognitive factors in intelligence. He suggests boldly that the purpose of the intelligence test is also to measure abilities hitherto considered as traits of personality. Wechsler argues that, since personality traits enter into the effectiveness of intelligent behavior, these traits must be included in any general, or "global," conception of intelligence. They are an integral part of our attempt to infer the adjustive capacities of an individual as a person. Wechsler cites evidence that he believes supports his contention that such factors as curiosity, impulse, instinct and temperament are basic to general intelligence, and that such factors constitute the "impure residue" mentioned previously.

Contemporary theory is therefore still not satisfied with its conception of human intelligence; it is beginning to suggest that non-

intellectual or "emotional" factors should be considered, not as extraneous and independent, but as entering into the composition of intelligence itself. Therefore one always has to state clearly whether one is concerned with intellectual factors in behavior or with intelligent behavior.

If we now turn to the history of animal psychology's approach to comparative intelligence, it will become evident that there has been a similar evolution of thought. The history of comparative psychology's attempts to study the intelligence of animals begins toward the end of the 19th century, also under the sanction and impetus of evolutionary biology. Evolutionary theory emphasized a continuity of structure and behavior in animals and men.

One, if not the main, reason for the early studies was to show that animals have minds too, or that consciousness is not limited to man. Nineteenth-century thinking equated consciousness mainly with cognition, which subsumed sensation. Sensation was the raw material of experience and learning the sufficient means of organizing sensations into knowledge. One might suggest that it was such ideas that predisposed students of animal psychology to reduce animal consciousness, or intelligence, to the problems of learning and sensory discrimination.

The classical study that can be said to have started experimental animal psychology was Thorndike's study in 1898 of how dogs and cats learn to get out of puzzle boxes. Small in 1901 made an exten-

sive study of rat behavior and started the vogue for rat-in-a-maze studies. Discrimination boxes were made to study the sensory functions. Testing for the presence of color vision in animals became possible with the invention of a special discrimination box by Yerkes and Watson in 1911.

This approach had the great advantage of intelligibility and of promoting experiment. Its over-simplicity, moreover, had another advantage, for the prompt reaction led animal workers to recognize, more quickly than the human testers, the extent of the problem of attacking the "higher" mental processes. It is a most interesting fact that the debate begun by Thorndike and Hobhouse about the turn of the century, has been the central issue of psychological theory since that time; and that theoretical discussion of the higher mental processes has depended almost entirely on the evidence, not of man's intellectual performance as one might have expected, but on that of animals.

In Thorndike's study, animals appeared to be able to behave something like human beings, but there was nothing that did not seem to be mechanical, or trial-and-error. Such studies produced an immediate reaction. It was protested that animals had to be allowed to perceive the relations among the parts of a problem situation before they would be able to demonstrate intelligence. Hobhouse, in a brilliant series of experiments, devised new problems, and tested a variety of

animals, to show that the apparently mechanical problem-solving studied by Thorndike was a product of the situation that he had used, allowing the cat no possibility of showing what intelligence it had. The problem is to choose a task that is suited to the animal studied. Hobhouse showed that the way in which a cat gets out of a complex problem-box may tell us less about its intelligence than the way in which it gets meat off a high shelf.

Both of these approaches were, and still are, important. Thorndike's study was in a different way as brilliant, or more brilliant than Hobhouse's, and though it is now generally conceded that Hobhouse, and later Kohler, refuted the main implication of the early "trial-and-error" theory, the general line of theorizing in Thorndike's work is still vigorously evident in modern learning theory.

Both views are important, also, for the present discussion. The first conceived of intelligence as some sort of integration of simple mechanical learning. The other conceived of intelligence as a special process in learning.

Lashley had recognized in 1929 that one method of identifying intelligence might be by studying the intercorrelations among specific animal abilities; and he had noted that his own work dealt only with some learning problems. His results are interpreted as reflecting the neural basis of intelligence as he argued, as Tryon did later, that the formation of maze habits involved processes characteristic of intelligent behavior. Lashley referred to intelligence as an intellectual factor.

Learning as an intellectual process had to be shown to be independent of the means of showing it, that is to say, the movement of fins, paws or hoofs. Jenkins, for instance (cited by Maier and Schnierla, 1935), designed a Thorndikian puzzle-box that did not depend on the animal's dexterity; chance solutions, of course, still occurred. And cognition must also be considered to be independent of specific sensations: Tryon (1942), working with rats, has shown that maze performance is independent of sensory acuity or of "stimulus - response connections." He concluded that his maze measured the capacity to develop "abstract spatial relations as defined by the maze path." This conclusion was the result of studying two types of rats that had been bred into separate strains: "maze - bright" and "maze - dull."

However, after the fashion of Hobhouse, one could say that the perception of relations was the mark of intelligence. Kohler (1926) showed among other things how an ape would put two poles together and suddenly, "insightfully," go across the cage to retrieve a banana which he had not been able to get with either of the poles individually. Although these studies have real merit in analyzing the cognitive functions independent of human cultural factors, the study of factors that make for individual differences is not popular with the "insight" approach to intelligence.

Rats were also found to be capable of insight or "reasoning." Maier (1932) showed that the rat could combine habits with a proficiency

"independent of the learning ability manifested" in the situation. Tolman and Honzig (1930) arranged an insight situation in which rats blocked from taking the shorter routes to food showed that they tended immediately to choose the next best route. This type of research on the higher mental processes, tends to yield all-or-none type of data. The intention seems to be to prove that animals are intelligent, not to find out how intelligent.

But if intelligence is a term for dealing with a more general feature of behavior, then it is a general factor, or set of factors, to explain why the behavior is efficient, and should mean more than, but include, what the organism may have learned or how the organism learns. For example, Searle (1949) recently studied some rats from Tryon's two strains and found the Brights to be food-driven, timid in open spaces, to have a "least distance" tendency, and so on. The Dulls were uninterested in food and had a specific fear of certain features of mechanical apparatus. He concluded that the differences between bright and dull rats were largely differences in motivational and emotional patterns. He suggested further study to isolate the differences in "cognitive" tendencies, not realizing that it might be at present a pseudo-problem. The identification of intellectual factors in intelligent behavior may be at least a problem in statistical factor analysis. The characteristic processes of intelligent behavior in the maze may be, in the main, emotional, as Searle's work indicates.

Recent work by McBride and Hebb (1948) illustrates how comparative psychology has come to recognize, as Wechsler has, non-cognitive features of intelligent behavior. They attempted to judge the intelligence of porpoises, limbless creatures unsuited to conventional test situations and yet which showed in other respects a complex level of behavioral organization. This animal's fears, sexual behavior and play are as elaborate as that of a chimpanzee, if not sometimes more complex. They conclude that we may have <u>assumed</u>

> "... the greater intelligence of primates - or what amounts to the same thing, have recognized it intuitively, and still cannot put the basis of recognition into words.... The difficulty with animal intelligence is that no very consistent correlation has been found between level of phylogenesis, and level of learning and problem-solving. A better correlation may exist with emotion and motivation. The chimpanzee's relation to man, for example, is best seen in such things as a temper tantrum..., or the simulation of friendliness by a malicious chimpanzee, until the victim is within reach. In no purely intellectual performance is the closeness of man and anthropoid so well demonstrated" (p.120).

And perhaps similar to Wechsler's concern over the factor of instincts in intelligence (1950) is Beach's (1950) emphasis on the developmental problems in instinctive behavior, which is one of the adjustive capacities of an organism. Beach cites, for example, the fact that female rats tend to show a grossly inefficient "maternal instinct" if self-grooming is precluded in development. He concluded that the development of "instinctive" patterns probably "involves processes of which current theories take not account. What these processes may be we shall not discover by continuing to concentrate on learning as we are now studying it " (p.122).

A methodologically more satisfactory way of measuring animal intelligence may be to use a Binet-type mixture of problems. Hebb and Williams (1946) gave animals a variety of problems in which both "direct perception and immediate memory items," as in the Binet-type test, are the basis of the intelligence rating. For rats, the method is one in which the rat is first accustomed to the kind of problem and the setting in which he must solve it. The problems themselves are easy: that is, unlike the alley maze which may take 50 to 100 trials, these problems can usually be solved in 5 or 10 trials and frequently in two or three. Motivational and emotional variabilities are at a minimum because of the rat's familiarity with the situation. Each problem is a particular set of barriers arranged in a closed field with which the animal has been accustomed. (This "closed-field" test was used

in the present investigation; the details of the procedure are described later under Experimental Methods, p.45).

Using this type of test, scores have been shown to be related to the type of situation in which the rats are reared: a complex and large living enclosure produces more "intelligent" adults than the conventional small rat cage (Hebb, 1947; Hymovitch, 1949). Some results appear to indicate that early exposure to a freer environment is of greater importance than equivalent opportunity later. The actual processes involved in such long term development have been ignored in the main by modern experimental theory (cf. Beach, 1950; Orlansky, 1949).

Comparative psychology is on the verge of attacking these long-term developmental problems thoroughly; it is proper that it should, for its results are then more likely to help in understanding the human organism. The behavior of adult man, perhaps more than of any other animal, is organised by the rich experiences to which he is subjected. One important problem for physiological psychology is now to reconsider the material on brain function in the light of this new emphasis. Such a reorientation of approach may help to make the results of brain damage studies of some relevance to the human problem. We may now turn to the experimental work on the physiological basis of animal intelligence and see what some of its problems have been.

Around the middle of the 19th century, Flourens, who initiated the chief method of experimental study of brain function, also initiated one of the two main lines of thought in the field by his emphasis on the non-specificity, or equipotentiality, of parts in the higher neural structures. He explored the separate effects of removing the cerebral lobes, the cerebellum, the medulla and the colliculi, from pigeons, rabbits and dogs. He concluded that,

> "The cerebral lobes are the exclusive origin of the sensations, perceptions, and volition.... The cerebral lobes, the cerebellum and the corpora quadrigemina can lose part of the substance without losing their function. They can regain them after having lost them completely. ....all of the essential and various parts of the nervous system have specific properties, ...and in spite of this marvellous diversity of properties, of functions...., they constitute nevertheless a unified system. When one point in the nervous system becomes excited, it excites all others.... There is community of reaction. Unity is the great reigning principle." (in Dennis, 1948, p. 139)

The second main line of thought, which can be called the hypothesis of localization of function, appeared in physio-

logical research when it was found that different parts of the cortex might have different functions. To find any specialization of areas of the cortex meant a return to something like the phrenology which Flourens had argued against so effectively. Fritsch and Hitzig discovered, in various animals, a motor area of the cortex, which when stimulated caused contralateral limb movements. Independent of each other, Panizza and Hitzig found that animals became blind when the occipital cortex was removed. The latter conclusion, however, was disputed for many years and was not conclusively demonstrated until Minkowski's systematic work appeared in 1917. Experimental and clinical observations began to indicate similar independent specialized cortical regions associated with other types of stimuli: touch, auditory, and so on.

The then contemporary learning theory, associationism, had assumed an almost infinite variety of ideas in the mind. Histological research demonstrated the intricate and fine cellular structure of the brain; since associations were between sensations and not motor, the rest of the cortex was called association cortex - where all the associated ideas probably were. And somewhere around the parietal or frontal lobes, where association cortex is greatest in extent, one could expect to find intelligence. Flechsig thought that, since the "sensory" areas surrounded the parietal association cortex, lesions there would produce dementia. Munk argued that intelligence was the aggregate functioning of all the sensory fields

and their interconnections. But Von Monakow found that frontal lesions produced no change in the psychic behavior of his dogs and monkeys and concluded that all the cortex except the frontal areas was involved in intelligence. Munk had implied that the frontal areas were part of the associative interconnections; Von Monakow approved the general idea but excluded the frontal lobes and added an emphasis on motor function as a component of intelligence. Intelligence, from the latter point of view, was the coordination of many diverse motor and sensory fields distributed throughout the cortex.

Other workers put the locus of intelligence elsewhere. Bianchi described his dogs with frontal lobe lesions as "weak-minded" and suggested that the frontal lobes were the organs of intellect. Hitzig agreed with Munk that "intelligence, or more correctly, the store of ideas", may not be in any special area, but emphasized that the frontal brain was the organ of abstract thought.

These conflicting interpretations and guesses were partly the result of inadequate inspection of lesions and partly the lack of controls. But the crucial point was that no one paid sufficient attention to the problem of trying to obtain a precise description of the behavior on which the controversy centered. At the turn of the century, Franz made a significant methodological contribution in bringing the apparatus of animal psychology to bear on the prob-

lem of what happened after cerebral lesions. He operated on cats and monkeys and studied their behavior in the puzzle-box; he concluded that the frontal lobes were the locus of the habit studied. Bilateral lesions resulted in a loss of the habit; but an animal could relearn to solve the puzzle normally after the operation. Such results, of course, tended to favor the theory of localization of function; but Franz did not use the term "intelligence" in his reports, and remained sceptical of any work that was supposed to show that mental processes could be localized in the brain.

Lashley, for a time a student of Franz, started in 1917 his thorough and systematic study of brain function in intelligence with the white rat. His Brain Mechanisms and Intelligence of 1929 summarized the work up to that date. He appreciated the difficulties in dealing objectively with the problem of intelligence, and tended to conceive of it as a unitary general capacity. His work centered on the rat maze as a method of studying habit formation, and retention, from which to infer the processes characteristic of intelligent behavior. Lashley's earlier work was an assult on learning, reified as cortical connections or as lowered resistance in synaptic chains. His later work helped establish the hypothesis that the maze measures more than sensory discrimination, and more than learning - as defined by the then popular conceptions of learning as stimulus-response bonds or complex reflex arcs.

Besides four types of mazes, Lashley used an incline box (for testing somesthetic sensitivity), a brightness-discrimination box, and a double-platform problem box. He explored the relationships between brain damage and various scores of learning and retention, with the lesions varying in size and locus in the rat's cortex.

The capacity to form or retain maze habits was found to be reduced in proportion to the amount of cortical tissue removed, independent of the locus of the tissue, the relationship being clearest on the most difficult mazes. The simple brightness-discrimination habit could be learned even in the absence of the striate cortex. This visual habit is somehow dependent upon striate cortex when it is learned by the normal animal, and yet is formed just as readily when the striate cortex is absent. Subcortical centers are presumed to take over the function in the absence of the striate tissue. In the double-platform box the results were that frontal lesions abolished the habit, while lesions up to 50 per cent in any part of the brain did not interfere with the formation of the habit. Lashley suggested that mass action did not apply to the results from the double-platform box and the brightness-discrimination box because of their"psychological simplicity". Since retardation in maze learning was not the result of sensory defects, he concluded that the formation of the maze habit involves processes characteristic

of intelligent behavior. Like Flourens, Lashley concluded that for maze learning the cortex works as a whole; this process is called "mass action" in maze learning or intelligence.

More recently, Lashley (1935) studied the relation between brain damage and the behavior of the rat in latch-box situations. Except for one box, "operated by the running and climbing movements of the animal", the retardation in learning compared to normal was proportional to extent of lesion. The first box mentioned above confirms the previous results with the double-platform box: both are psychologically "too simple." Retardation as a result of anaesthesias produced by cord lesions or receptor deprivation was not as great as the retardation in learning as a result of cortical lesions judged as producing equivalent anaesthesias. The retardation was ascribed to limitation in exploratory acts, failure to develop movements specifically adapted to manipulate the latches, reduction in time spent in exploring separate items in the situation, and sensory deficiency.

This mass action type of relationship has been found in other research. Krechevsky (1937) found that only the size, not the locus, of a lesion predicted the decrease in number of different choices made, when rats were offered several equal-length paths to the goal. Ghiselli (1938) showed that lesion size correlated with retardation in learning the multiple-unit discrimination box, a

maze in which light intensity indicates the correct path.

All this work is oriented toward an interpretation of intelligence as a capacity for learning, independent of particular sensations or specific motor skills. The mass-action effect is interpreted as indicating that there is a factor in the action of all cortical tissue which is independent of any of the sensory functions of the tissue. Comparing the effects of peripheral blinding and striate removal on maze performance, Lashley (1943) concluded that the greater retardation in the cases with "central" blinding indicated that the visual cortex had a function exercised in the absence of any visual stimuli.

But in the learning of difficult visual discriminations, rats with damaged striate areas tend to show an all-or-none capacity (Lashley, 1939, 1942). Lesions outside of the visual area do not affect this learning, unless the animal has motor-area lesions. (These latter rats readily jump to simple patterns and appear to have no defects of vision.) "In general, either the animal made no improvement during 300 trials of training or his learning score fell within the normal range" (Lashley, 1942, p. 219). This complex learning therefore demonstrated an "autonomy of the visual cortex": in one or another case all other parts of the cortical tissue were interfered with. The habit appears to be learned or not learned depending solely on whether the binocular field area of the striate

tissue remained intact. Lashley reasoned that if the excitation is to have a final influence on the motor cortex for adaptive movements, then it must interact with other parts of the neopallium, or work through diffuse connections with any cortical field remaining intact, or traverse subcortical regions. The latter alternative appears to be favored by Lashley (1942).

This interpretation would appear to emphasize thalamocortical systems more than intracortical systems as the essential feature of brain function, which is in keeping with the physiological and anatomical evidence. Therefore one can infer that mass-action effects occur because one interferes with integration in various thalamo-cortical systems, not because one interferes with integration in intracortical systems. Lashley's student, Tsang (1937), appears to express a different emphasis. Tsang studied the effects of diagonal hemidecortication (cortex removed from anterior half on one side, posterior half on the other side). The greater deterioration resulting from diagonal hemidecortication, as compared with the removal of a more compact mass of cortex, indicated that "the efficiency of a complex and general function is conditioned by the mass of nervous tissue available, in so far as the available mass is so situated to assure a full degree of mutual facilitation among its parts" (p. 244). The mutual facilitation for mass action would appear to be more of an intracortical function in Tsang's experiment.

And therefore one might be inclined to lend some weight to the second of the alternatives in the explanation of "autonomy of the visual cortex." Excitation may work through diffuse connections with any cortical field remaining intact, in its subsequent influence on the motor cortex.

Such considerations may have been instrumental in causing Lashley to change his conception of intelligence. In 1938 Lashley took special note of the fact that animals with severe lesions in the striate cortex may learn to choose the larger of two circles as quickly as do normals, but are unable to learn the normal discrimination of the larger of three circles. On the basis of such data and the qualitative differences in perceptual abilities in different species, he suggested that the different kinds of abstraction may have entirely different organic bases, that the development of intelligence involves the addition of qualitatively different processes and that the faculty of general intelligence may be an artifact due solely to growth processes. There would seem to be the implication that the different processes added would depend primarily on new thalamo-cortical systems. In his recent work (1948) where he failed to find symptoms of agnosia in monkeys with extensive prestriate lesions, Lashley again appears to indicate that a thalmo-cortical system, the pulvinar-cortical, would have to be the system involved, if there is one system, in the production of visual agnosia. This may mean that the pulvinar-cortical system is of special impor-

tance in normal complex visual perception.

Lashley may therefore be understood to imply that cortical mass is the important thing for some abilities, and particular areas, or systems for others. He has not indicated what the abilities comprising intelligence may be, other than the ability to abstract.

Other research workers in physiological psychology have not theorized as extensively as Lashley on the physiological basis of intelligence, but some of their research deserves mention as illustrative of certain problems.

Krechevsky (1935) studied the effects of cortical lesions on the tendency of rats to adopt different kinds of "hypotheses" in a maze. Adopting a "spatial hypothesis" meant that the animal looked for food in the right alley or the left alley, or the like; a "visual hypothesis" meant a tendency to enter a light or a dark alley apart from its position. Normal animals tend to vary periodically as to the hypotheses adopted; the operated rats were more frequently found to adopt one consistent mode of behavior. Two separate cortical areas were found; destroying each of these bilaterally interfered with the appearance of one type of hypothesis. Since the "visual-hypothesis area" was largely visual striate cortex, the relationship appeared reasonable in some respects. Lashley has attempted to argue that this may be related to types of sensory functions (1945). On the other hand, one might suggest that there

were two different types of emotional reaction in relation to visual stimulation; all of the rats had at least brightness vision and generally some striate tissue. Perhaps after the fashion of Searle (1949) it would be possible to show emotional rather than intellectual differences as being the key factor in the differences of intelligent behavior. "Attitude," that is, would be as good a term as "hypothesis."

Krechevsky was probably surprised to find (1937) that although minor brain lesions reduced the rats' variability (number of hypotheses manifested) and made them stereotyped, the preference could be changed in special circumstances. He had considered "spontaneous" variability as possibly more fundamental than learning, and seemed to consider it some sort of cognitive process: his research was supposed to indicate something about the nature of rat behavior when rats learn which are possible solutions and which are "wrong" solutions. More recently, he has recognized that such situations require a consideration of the emotional reaction of the organism: "The stronger the tension, the stronger the emotional "tone" of the situation, the less likely that cognitive reorganization will occur" (Krech and Crutchfield, 1948, p. 141). It is possible then that the brain damage changes the emotional tone of the problem situations for the rats.

Maier (1932) showed that rats in the reasoning situation

(see page 11) were retarded when given minimal 10 to 18 per cent cortical lesions, and the "reasoning" behavior was abolished with lesions over 18 per cent; locus of lesion was not a factor. It was concluded that the rat must put together his "general knowledge" of the maze to show "reasoning." It was assumed that the operated rat had lost some knowledge or could not reason. Consideration should also have been given to the possibility of describing the changed behavior in other terms. Harsh (1937) has even suggested that emotional factors enter into the reasoning of normal rats. The neural systems that are hypothesized as the basis of intellectual performances are certainly not completely separate from what happens in the nervous system when an organism is emotionally disturbed. If one is solely interested in those features of brain activity that are the basis of cognitive or intellectual abilities then all other conditions in the nervous system theoretically must be controlled. Since the operated animal is a radically changed animal we must be very careful about deducing changes only in intellectual functions. Perhaps we need first a term - like intelligence - which will represent the total efficiency of the organism in a problem situation, a term that includes emotional and intellectual adjustive capacities among others.

A consideration of the interrelationships between emotional and intellectual factors becomes more important in the

interpretation of the studies on frontal lobe function. Jacobsen (1936) showed that prefrontal lobectomized monkeys were not able to solve a delay problem normally. They could not remember which cup of two had had food placed under it, if they were required to wait more than one or two seconds. Normal animals can delay up to 30 seconds. In addition to this, it was noted that chimpanzees when operated upon did not go into temper tantrums upon making a mistake. Normal animals, on the contrary, become considerably annoyed. Further work, by Finan (1942) on monkeys, showed that by administering sedatives the performance could be improved; he concluded that they must have a difficulty in "attention." Malmo (1942) turned out the lights during the delay and improved performance to normal; he concluded that "attention" was important and that the animals might be considered as oversusceptible to interference effects from sensory stimulation. The interference effects are considered to be similar to those assumed to underlie retroactive inhibition. Morgan and Stellar (1950) conclude that cutting down interference leads to an increase in "memory," but do not attempt a similar approach to Lashley's report of the same disturbance of delayed response in cases with the prestriate cortex removed (1948). Settlage, Zable and Harlow (1948) using a similar experimental situation concluded that animals with frontal lobectomies suffered from perseverative interference, "i.e., from impairment of the

ability to relinquish previously acquired, interfering reaction patterns;" but they had no prestriate control operations. The most interesting report is that of Blum (1948) which showed that his chimpanzees without prefrontal lobes could do the delay problem.

Since Blum's chimpanzees successfully performed the delay problem, it has been suggested that something like scar formation, with its accompanying "epileptoid" dysfunction, may be a cause of much of the observed effects of removing the frontal cortex. That is to say, some active neural disturbance may be the factor that produces the emotional and intellectual changes. Finan's sedative may have reduced these disorganizing effects. Blum, Blum and Chow (1948) reported on a monkey with frontal lobes removed and showed that the administration of benzedrine can produce a unilateral epileptiform convulsion from otherwise "quiescent" foci. It may be suggested too that often the frontal lobectomized animal has some form of "subclinical" focus of disturbance that is producing the modification of behavior.

The research on delayed response was considered to be one of the most promising fields of investigation: the ability to delay was a specific higher capacity, definitely localized in the frontal lobes. Now, unfortunately, it has disappeared and turned up in the back of the head, and will probably continue its career as a problem in memory and attention.

Perhaps the cognitive terminology should be replaced by a purely physiological terminology or accompanied by terminology referring to the other aspects of the human mind, as feeling and emotion. Research oriented toward measuring the non-intellectual factors in an animal's behavior may help considerably, in addition to the intellective approach, in explaining why an animal actually does behave in certain ways when part of his brain is removed.

The problem of dealing first with the animal or its brain as a whole, is probably even more pressing when we consider the differential effects of early and late brain damage. Animal work has consistently found that brain damage in infancy is less effective, in changing adult behavior, than comparable adult damage. Lashley (1938) concluded, on the basis of Tsang's work (1937), that adult maze performance suffered as much from an 8 per cent cortical lesion as from a 40 per cent lesion made in infancy. Beach (1938) found that cortical lesions, which in the adult interfere drastically with the rat's maternal behavior, essentially have no effect when performed in infancy. Although lesions in the motor cortex can produce long-term paralyses in the adult monkey, Kennard (1936) showed that there was an insignificant paralysis from similar lesions in the infant macaque monkey. Tsang (1937) studied the effect of removing visual striate cortex in young rats and his data are suggestive of the presence of pattern vision in the rats at maturity;

such operations performed at maturity definitely abolish pattern vision. Lashley (1938) considered these differences as having two possible explanations: (1) destruction of the higher cortical centers prevents the normal regression of capacities of lower subcortical centers during development, or (2) long-continued training can restore general capacities, during the developmental period. This problem of the different effects will be considered further in the following discussion of the human problem.

The research on effects of brain damage on human intelligence may be considered first in general terms in relation to earlier discussions. Klebanoff (1945) surveyed the literature up to 1941 and commented,

> "The results of the psychological investigations employing unspecialized tests of formal intellectual ability lead to one of two paradoxical conclusions. One might accept the findings.... and agree that there is no observable or demonstrable intellectual defect that occurs where there is the structural potentiality for a transference of functional ability. To put it specifically, it may be said that there is no detectable alteration in the intelligence of such patients. The second conclusion, possibly more tenable, would hold that disease or removal of cortical tissue always

results in some deficit in the intellectual sphere, but that this functional loss cannot be demonstrated through tests of general and formal intelligence. In this view, the nature of the intellectual defect would be conceived of as being a highly subtle and elusive one which requires the breakdown of "general intelligence" into its component parts. Such an analysis of intellectual functioning must be made in these cases before one can conclude with certainty that there is no loss of intellectual ability..."(p.599).

Perhaps the difficulty has been in assuming that there must be some intellectual defect whenever a human being loses some cortical tissue, and in assuming that good intelligence tests would indicate any "intellectual" changes. As a result of the popularity of mass-action theory it is not recognized that the animal work does allow one to suggest that considerable cortical tissue can be removed and have no effect on quite complex behavioral functions.

Some of the difficulties of interpreting the human clinical data may be mentioned first. Anatomical data may be absent, or grossly inaccurate. Autopsies may not be permitted, and in any event the patient often lives for many years after the research is reported. The neurosurgeon's estimate of the extent of damage,

with the best of intentions, can be distorted by various factors: for instance, diffuse pathological changes may have affected other parts of the brain and not be observed, or in the case of tumors, the brain may be considerably displaced, so that landmarks are unreliable. Further, it is very difficult to obtain the consent of normal subjects to be tested (Weisenberg, Roe and McBride, 1936), so that the normal-control method has not often been used successfully in the study of human brain damage. Useful data may be obtained by preoperative testing for comparison with results after operations; often, however, there may not be opportunity for this. In some cases the removal of pathologically affected tissue results in improvement over the preoperative morbid condition, showing that it is sometimes impossible to assess the effects of removal of neural tissue even by pre- and postoperative comparison. Klebanoff's (1945) review collected most of the few intelligence test reports that had been reported on brain-damaged patients. Most of the research was done on cases with frontal lobe damage; no reliable changes in general intelligence were reported.

Hebb (1945) reviewed the literature on frontal lobe function and concluded that no single higher function had been proven to depend on the frontal lobes. But Malmo (1948), using the Wechsler-Bellevue test pre- and post-operatively, reported reduction of general intelligence including the vocabulary scores,

following bilateral frontal gyrectomies and lobotomies. He concluded that the effects were not related to locus or size of lesion, or tissue dysfunction. Recently the Columbia-Greystone Associates (1949) reported an elaborate investigation of the effects of operations on the frontal lobes. The operations involved the removal of various parts of the frontal cortex in an attempt to cure the mental illness of 24 psychotics; considerable care was taken with regard to all types of controls (except for operating on other parts of the brain). A large battery of conventional psychological tests was used. The general finding was that the operations resulted in no permanent intellectual changes, either in the Wechsler-Bellevue intelligence test or in other intellectual tests. Landis, Zubin, and Mettler (1950) concisely summarized the results:

"1. We have no evidence of any permanent intellectual damage brought about by clean, uncomplicated surgery done on the prefrontal and orbital (granular) portions of the frontal lobes. ...Removal of Area 44 (Broca's area) produced no disturbance in speech.

2. There is no evidence that such mental abilities as learning, memory, or association are changed or altered in any permanent fashion...

3. We obtained no evidence of loss or gain in creative

ability, imagination, or high level achievement. We obtained no evidence of loss or change in social or ethical attitudes nor in humor.

4. ... various projective tests... disclosed... no change.
5. The comparison of performance before and three months after operation with a wide variety of methods failed to show any regular alteration in the ability to generalize or to abstract... (p. 130)"

Transient effects were noted, however. The Porteus maze test showed the most marked transient effects. This pencil maze test has been supposed to test foresight and ability to plan. Return to normal level of performance on this test appeared to parallel the social recovery of the patients. This result may indicate that the operation broke "up old habits of social adaptation and planning," and that there was subsequent formation of new, more socially acceptable, habits. Landis, et al., (1950) suggested cautiously, that the third of the patients that are improved by the operation, showed a decrease in "vigilance, anguish and zeal." The performance tests of the Wechsler-Bellevue test gave some indication of being affected (particularly Object Assembly) and the effect appeared to be related to Brodman area 8 ablations. This susceptibility of the performance tests has been noted before (Hebb, 1942; Weisenberg and McBride, 1935) and has served to emphasize that the more verbal aspects of intelligence are the factors which tend to

remain unimpaired in brain damage. This is despite the fact that verbal abilities are the distinctly human feature in mammalian behavior and the popular opinion that the frontal cortex has attained maximum development in man and "phylogenetically is the most recent acquisition."

On the other hand Halstead (1947) surveyed the "psychological" theories of intelligence and found that none made specific "provision for consciousness as a component of intelligence... the ramifications of this omission in contemporary ethical and moral philosophy... have been great indeed"(p. 105). He discarded these and the impressionistic neurological theories and made a new battery of tests to measure "biological intelligence." This battery was subjected to a Thurstone factor analysis and administered to various patients with brain damage. The subtests may be classified as either complex visual field tests or performance tests; the validity of the test rests upon internal consistency. Halstead constructed an index of impairment, independent of language functions, which was shown to be greatest after loss of frontal lobe tissue. The impairment was not as severe after injury in other brain regions and unrelated to apparent extent of lesions. Halstead's lack of controls, particularly for age, has been criticized (Hebb, 1949). Since the external validity of the tests is not clear, the connection between the non-language function of these tests and man's "highest reaches of

intellect" and "ethical and moral philosphy" remains rather obscure.

Research on other parts of the human brain in relation to performance on general intelligence tests is far behind the work on the frontal lobe and the results require even greater scepticism.

Too often the clinical psychologist excuses a patient's poor performance on an intelligence test because the patient has some apparent sensory or motor deficit; and consequently reports of such defects often do not get into the literature. This is the result of equating intelligence with cognition, and so has to be distinct from sensory factors. Such material would be particularly useful in the discussion of our next topic.

Of equal importance, but with even less information available for its solution, is the problem of how brain damage affects the development of adult intelligence. This raises for consideration first the problem of aphasia, which appears to interfere drastically with all subtests, verbal or performance, of the intelligence test; frequently, however, one or two performance subtests are unpredictably preserved (Hebb, 1942). Hebb inferred that adult brain damage could be regarded as affecting adult abilities selectively and that there would probably be something like a bimodal distribution of subtest scores of the intelligence test in brain damage cases: cases in which verbal subtests are preserved (non-aphasics) and cases in which some performance subtests tend to be preserved (aphasics).

Analysis of a selected group of test scores of brain-damaged children yielded no bimodal pattern of scores; the scores of these non-aphasic cases showed a lowered vocabulary score. Hebb concluded that apart from the effects of aphasia, sensory and motor defects, early brain damage was less selective and more generalized in its effects and tended to affect verbal abilities more. Strauss and Lehtinen (1950) surveyed the literature on exogenous and endogenous mental deficiency in children, and concluded that standardized intelligence tests do not distinguish qualitatively between brain-damaged children and mental defectives when they are matched for IQ. They are both better on the performance tests. Strauss and Lehtinen also showed that the brain-damaged children do not benefit, as mental defectives do, from the best of training in so far as IQ is concerned: the IQ continues to decline. This lends weight to the suggestion (Hebb, 1942) that during development a greater stress is placed on the cerebral tissue as a whole for the emergence of intelligence than is necessary for intelligent behavior in the adult; intelligence in fact does not seem to depend on all the cortical tissue in the adult. This material on infant brain damage is deficient in the lack of anatomical data, but provides the only data available on this problem.

From such considerations in the main, Hebb (1949) developed a conceptual scheme which may be briefly summarised as: in general, repeated stimulation leads to the formation of systems of neural

organization ("cell assemblies"), that may become autonomous. Short-circuited sets of these neural systems develop ("phase sequences"), independent mainly of specific cell assemblies; such sequences form the basis of conceptual activity and complex behavior. Early brain damage is construed as interfering with the development of the numerous basic cell assemblies to the extent of limiting the background for later development of phase sequences (and intelligent behavior). Adult brain damage may not seriously interfere with the phase sequences (and intelligent behavior) if several alternate organizations of cell assemblies could now serve to maintain them, or function as their equivalent.

Unfortunately there is no direct evidence in experimental physiology to support this contention; one suggestive line of evidence is an experiment comparing the effects of early vs. late enucleation on adult rat problem-solving behavior, which showed an advantage for the adult enucleated group (Hebb, 1947; Hymovitch, 1949). The visual experience is considered to have set up during development neural systems that manifested themselves independently of their sensory source. The differences between the early and the late groups are not reliable, however, and it has not been checked as to whether these animals showed differences in growth rate as reported by Browman and Browman (1944). (Rate of growth and age of sexual maturity were retarded by early enucleation and shown to be largely

counteracted by administering regular injections with a saline extract of bovine retinae.)

However, there was a suggestion in Hymovitch's work that the advantage of late enucleation was greater when the groups of animals were reared in a complex environmental situation: greater variety of visual stimulation would theoretically be more likely to develop a significant number of the hypothetical neural systems that are assumed to be able to operate independent of the sensory source. The work on the comparison of the effects of early and late brain damage on rat behavior may now be reconsidered.

The effect of early brain damage on adult rat behavior has been found to be less than that of late brain damage, which may be a result of the greater "plasticity" of the nervous system in the infant (Tsang, 1937). There appears to be substantially less interference with motor organization and sensory capacities. But even slight defects might interfere with the development of more complex neural organizations in a complex environment, such as are implied by Hymovitch's work on the lasting effects of the infant environment. The very small effects of infant brain damage on rat intelligence which others have reported may be small, partly, because the rats have always been reared in restricted circumstances. Rearing in a wide environment may show other effects.

There are other possible explanations of the facts, however.

The behavior of the adult rat may be proportionately less dependent, than in the human, on what the organism is exposed to during development. This suggested species difference may mean that complex adult behavior for the rat is mainly a function of the rat's sensory and motor efficiency; that is to say, the rat is more "stimulus-bound" than the human. Early brain damage in the rat may interfere less than adult brain damage with adult sensori-motor organization, and therefore interfere less with the intelligent behavior of the adult rat. Early brain damage in the human may interfere more than adult brain damage with the necessary neural organizations that underlie the complex adult human behavior.

In summary, present-day research gives hope that the psychological analysis of general intelligence will be able to advance much further as the research encompasses the non-intellectual factors in intelligent behavior. Physiological understanding of the factors in intelligence waits upon an adequate formulation of the psychological problem. Physiological analysis of human brain function in general intelligence has suffered from the difficulty of obtaining adequate data. Animal work, although more precise, does not at present help in the understanding of the physiological basis of general intelligence: in one respect it shows an almost direct reversal of the human evidence - early cortical damage appears to have little or no effect upon adult behavior, whereas in

the human the higher intellectual abilities appear to suffer more in cases of infant brain damage.

THE PRESENT INVESTIGATION

The specific purpose of the present investigation was to study the effect of cortical damage on rat intelligence under conditions which would be more comparable to those in which the human clinical data are obtained. For this reason a new measure of problem-solving was adopted, which on a priori grounds is more like an intelligence test than the alley maze which was used by Lashley. It was also necessary to take into account the environment in which the animal grew up, and the age at which the lesion occurred. Finally, it was obviously desirable to include a study of unilateral lesions, which comprise the great majority of human brain operations but whose effect on intelligence rarely has been studied in animals.

Previous research indicated that the Hebb-Williams (1946) type of test was able to detect differences in adult behavior as a result of rearing rats as pets, as distinguished from the normal rearing in a laboratory cage (Hebb, 1947). This effect of rearing in a more complex environment was confirmed in a laboratory situation (Hymovitch, 1949). The hypothetical resultant neural differences in the more intelligent pet rats appears to be related mainly to visual experience, and yet may also be presumed to be operative independent of vision, since differences of early experience are reported to affect the behavior of the blind rat at maturity.

Enucleation of the eyes in the infant is probably more deleterious than in the adult rat (Hymovitch, 1949).

Hymovitch has also shown that this type of test confirmed the general impression of psychologists, that early experience is of more importance than equivalent later experience. This experimental result is presumably related to the apparent difference in the effect of early and late brain injury which has been discussed earlier. Though it is not certain that Hebb's conclusions, based on clinical evidence alone, are right, it may be necessary to take account of the time at which brain injury occurs when evaluating its results. In the present study, accordingly, lesions were made in normal adult rats and also in infant rats.

SUBJECTS

The original subjects were 116 male hooded rats. Twenty-eight animals died as a result of operations. The results with 18 cases were discarded on the basis of necropsy study showing operative damage to subcortical structures, or lesions too extensive in other respects (e.g., some of the larger anterior lesions extended into the posterior half of the brain and so could not be treated as "anterior.") The results accordingly are based on the records of 70 animals: 13 normal and 57 operate.

EXPERIMENTAL METHODS

The general plan of the experiment was to operate upon different parts of the rat cortex, in one group at infancy and another group at maturity. During growth the animals were exposed to a complex environment shown by Hymovitch (1949) to contribute to the development of rat "intelligence."

All rats were given extensive handling throughout the experiment. From the 23rd day of age until the 119th day the rats were exposed frequently to the complex environment referred to above. Weaning occurred after the 30th day. The exposure to the freer environment was about two hours per day for the first week, thereafter almost 12 hours per day except for approximately ten days at the time of operating on the adult rats. During this period all rats were kept in their cages. Total exposure time to the complex environment was approximately 660 hours.

The complex environment consisted of two wooden boxes, each 42" x 48" x 8" high, connected by a passageway. The top of the boxes was made of $\frac{1}{2}$" wire mesh. The boxes contained food and water, and a variety of wire and wooden structures: low alleyways, maze-like sections, enclosures, and so forth. These structures gave the animals continuous experience in orienting themselves and finding their way among a number of objects.

When the rats reached 119 days of age, they were placed

in colony cages and fed only twice a day in the testing program. The test method was that described by Hebb and Williams (1946), and Rabinovitch (1949). In this test, the rat is first accustomed to handling and orientated with respect to a starting box and a goal box in an enclosed field. The closed-field box used in this investigation was a wooden box 30" x 30" x 4" high, with ¼" wire mesh for a top. Entrance and goal boxes were attached at diagonally opposite corners. After preliminary training has reduced fear and exploratory behavior to a reasonable minimum, 24 test problems are presented, in which the rat must pass simple barriers to get to the food.

All the rats had met a criterion (of 9 runs per minute of running time) in five days of preliminary training. The preliminary training was similar to the testing procedure: two problems were given each day, one in the morning, the other in the evening. After each test the rats were given extra food to maintain health. The test problems themselves are such that bright normal rats readily succeed in finding the most direct path to the goal, often on the first or second run, but the difficulty is great enough so that there is a great range of scores even among normal rats. Errors are recorded whenever a rat deviates from the direct path into designated zones of the field. The total number of errors and errorless runs are recorded for ten runs on each test. Emotional

and motivational disturbances occur only in relation to the nature of some of the later more difficult problems, since the rat is not tested until he is thoroughly acquainted with the procedure and the location of the goal.

SURGICAL AND HISTOLOGICAL METHODS

Operations were performed under deep ether anaesthesia with antiseptic technique. The cortical tissue was removed by suction through curved fine glass tubing. Infant lesions were made at 18 to 20 days of age and adult lesions at 74 to 76 days. The loci of the lesions may be classified as: bilateral posterior, bilateral anterior, and unilateral.

At the completion of testing the operated animals were brought to necropsy. The brains were removed, fixed, sectioned (at 40 micra) and stained with thionin. At least every eighth section was mounted, for the bilateral lesions; for most unilateral lesions, every tenth.

Reconstruction of the cortical lesions were made on the conventional Lashley rat brain diagrams (Lashley, 1929). However, the reconstruction procedure was modified somewhat in an attempt to overcome the tendency of the cortical tissue to fill in the operated area and so cause an error in the estimation of the extent of damage.

This reconstruction procedure involved mimeographing standardized cross-sectional diagrams corresponding to Lashley's levels 2 to 17. The extent of lesion in the corresponding brain sections was marked directly on these diagrams, using a projection microscope. The linear extent of pyriform cortex and isocortex

in normal sections appeared to have a reasonably constant relationship for any given level. Therefore, the appropriate magnification in the reconstruction work was judged mainly by matching the extent of pyriform cortex of a particular section with that of the diagram. This procedure enabled the experimenter to estimate what was the true extent of operative damage by attempting to offset the tendency of the brain tissue to fill in the lesion gap. This filling-in tendency appeared to be greater in the infant lesions (it may also have been more extensive because of the use of suction, as compared to the older thermocautery method of making lesions). The extent of damage indicated on the cross-sectional diagrams was transferred with proportional dividers to standard Lashley diagrams. The extent of the lesions was measured with a planimeter and expressed in terms of percentage of the total area of the isocortex.

The nature of the degeneration in the lateral geniculate nuclei of both the unilateral and bilateral posterior lesion groups was also determined. Diagrams of a standardized maximal cross-section of the nucleus were prepared (after Lashley, 1934). The nuclei were examined under the microscope and the diagrams marked to show the locus and amount of degeneration. Records were made of the condition of the anterior and posterior portions of the nuclei, shrinking of the nuclei, decrease in cellular density, scar formation and extent of degeneration of cells.

Difficulty in making these lateral-geniculate assessments was encountered in the early-operation cases, since early operations apparently tended to shrink the nucleus. The extent of degeneration was easiest to determine in the unilateral group, as the opposite side offered a normal nucleus for immediate comparison. Accordingly, the partly degenerated lateral-geniculate nuclei of the unilateral-lesion group were arranged in order of amount of cell loss. These 20 cases were then made the basis of a 20-point scale by which to assess destruction in the nuclei of the bilateral-lesion cases. Each nucleus of the bilateral-lesion cases was rated on this scale, and the ratings for the two sides of the brain were then added together to obtain a single value for the amount of lateral-geniculate destruction for each animal in the posterior-lesion group. Figure 1 illustrates the lateral-geniculate diagram and shows the method of marking the diagram for amount of degeneration.

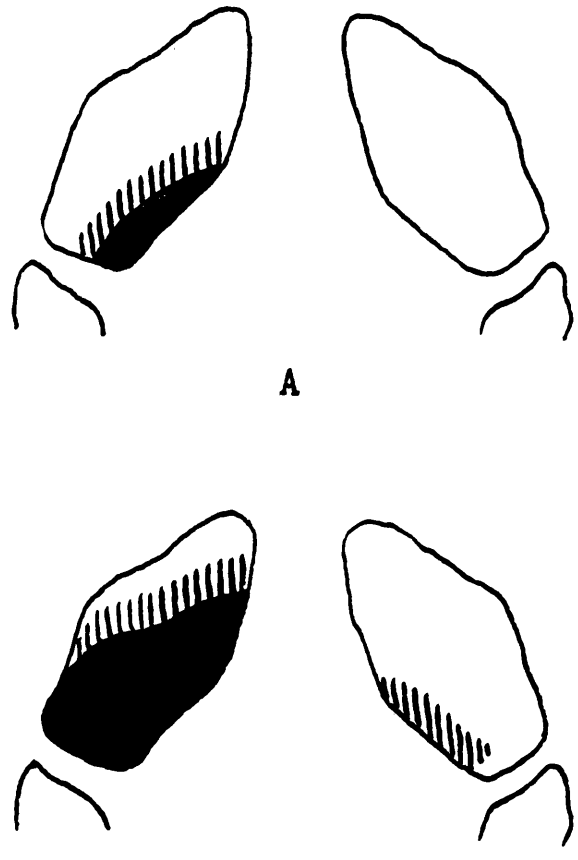

Figure 1. Cross-section of lateral geniculate nuclei, showing examples of extent of degeneration. The dark area indicates loss of cells; shading, decrease in cell density. A illustrates the extent of degeneration of the left nucleus following a late unilateral lesion, with degeneration ranked 3. B illustrates degeneration of the nuclei following an early bilateral posterior lesion: rank 11 on the left, 2 on the right; index of total degeneration, 13.

RESULTS

The results are classified according to the locus of lesion, anterior, posterior, or unilateral, and also according to the time of operation, early or late. Thus there are six experimental groups: early anterior, late anterior, early posterior, and so on.

Anterior lesions do not extend back beyond Lashley's level 9 and posterior lesions do not extend forward beyond level 8½. (Lashley divided the rat brain into 18 levels, each representing approximately one millimeter on the rostro-caudal axis of the average adult brain. Level 1 is the extreme anterior extent of the isocortex, level 9½ halfway from the anterior to the posterior extreme.)

The cortical damage in the anterior-lesion group did not involve the striate area and, according to Krieg (1946), may be considered as involving cytoarchitectural areas 10, 4, 6, 3, 1 and 2. These areas are conventionally called premotor, motor and somesthetic. The cortical damage in the posterior-lesion group in all cases involved the striate area and according to Krieg may be considered as involving areas 17, 18 and 7, the primary visual area and adjacent "associative" tissue. The unilateral lesions ranged over almost the full length of the brain; in all cases the striate area was involved.

Table I shows the means and standard deviations of the amount of cortical destruction in terms of percentage of the total

TABLE I

COMPARISON OF LESION SIZES AND ERROR SCORES
FOR VARIOUS GROUPS

Group	N	Percentage of lesion		Error scores		Correlation (r) of errors with lesion size
		$\bar{X}$	S.D.	$\bar{X}$	S.D.	
Anterior early	9	15.3	4.8	194.2	44.6	- .19
Anterior late	10	9.0	4.4	176.5	27.4	.06
Total anterior	19	12.5	5.3	184.9	37.6	.05
Posterior early	11	19.6	8.6	342.0	66.8	.49
Posterior late	7	15.0	10.9	410.0	169.2	.83
Total posterior	18	17.8	9.8	368.4	122.3	.58
Unilateral early	12	35.8	7.9	285.4	53.1	.33
Unilateral late	8	26.4	11.0	287.1	64.3	.77
Total unilateral	20	32.1	10.3	286.4	57.9	.50
Normal controls	13	-	-	194.0	42.6	-

TABLE II

ERRORLESS-RUNS SCORES AND CORRELATIONS WITH LESION SIZE FOR VARIOUS GROUPS

Group	N	Errorless-runs scores		Correlation (r) of errorless runs with lesion size
		$\bar{X}$	S.D.	
Anterior early	9	154.8	19.9	.16
Anterior late	10	160.7	8.5	- .05
Total anterior	19	157.9	15.3	- .03
Posterior early	11	116.7	15.0	- .44
Posterior late	7	94.1	43.7	- .82
Total posterior	18	107.9	31.6	- .52
Unilateral early	12	133.3	17.2	- .39
Unilateral late	8	129.5	24.1	- .82
Total Unilateral	20	131.8	20.4	- .52
Normal controls	13	157.7	16.0	-

TABLE III

DEGENERATION IN LATERAL GENICULATE AND RELATION TO ERROR SCORE

Lesion group	N	Degeneration		Correlation (r) of errors with amount of degeneration
		$\bar{X}$	S.D.	
Unilateral early	12	11.4	5.3	.29
Unilateral late	8	9.1	6.1	.62
Total unilateral	20	10.5	5.8	.44
Posterior early	11	28.0	9.3	.70
Posterior late	7	18.1	9.4	.87
Total posterior	18	24.2	10.5	.50

area of the isocortex, for each group of animals. Unilateral lesions as a group were much larger than the bilateral-posterior lesions, and bilateral-posterior larger than bilateral-anterior. In each of these groups, also, early lesions tended to be larger than late lesions.

Table III shows the means and standard deviations of the amount of retrograde degeneration in the lateral geniculate nuclei, the visual relay center of the thalamus. (Anterior lesions, of course, did not encroach upon the striate cortex and consequently did not affect the lateral geniculate.) In terms of the scale which has been described, there was twice as much degeneration in the lateral geniculates of the posterior-lesion group as there was in the unilateral group.

Direct operative damage to subcortical structures was negligible (cases in which there was such damage were discarded). Although there was degeneration in other thalamic nuclei besides the lateral geniculate, it was not assessed in this study. The reason for paying special attention to the lateral geniculate is that visual factors have considerable importance for test performance and the condition of the lateral geniculate is a more reliable indication of visual field defects than the locus of cortical destruction. Operation may damage the optic radiations without removing the corresponding cortical tissue.

Product-moment correlation coefficients for the various groups were computed between scores on the first half and scores on

the second half of the 24-item test. The values range from .57 to .93 for error scores and from .60 to .97 for errorless runs, when corrected by the Brown-Spearman formula. The correlations between total errors and total errorless runs range from .80 to .99 for the various groups. The test thus appears to have a satisfactory degree of reliability.

The means and standard deviations of the error scores are tabulated for the various groups in Table I, and of the errorless runs in Table II. The mean test scores of the anterior-lesion group do not differ significantly from the normal test scores (actually, the late-anterior group made <u>fewer</u> errors than the normal).

The test scores of the unilateral-lesion group are significantly worse than normal. The scores for the left-hemisphere lesions were not significantly different from those for the right-hemisphere, nor early unilaterals from late.

The group with the posterior lesions showed the greatest effect of operation. Within this group the animals with lesions made in infancy had the better test scores.

The first point of interest in these results is the lack of effect of frontal lesions on test scores. These lesions were smaller than the unilateral or the occipital lesions, but their size does not account for the lack of effect. By excluding the six largest lesions in the posterior group, a group of 12 posterior

lesions is obtained with a mean size of 12.3 per cent cortical destruction, compared to 12.5 per cent for the total anterior group of 19 animals. But the mean error score for the 14 animals with posterior lesions is 335, compared to 185 for the anterior group. The difference is highly significant. This is despite the fact that the volume of cortex destroyed is greater for the anterior group in this comparison: the determination of size of lesion is in terms of area, and much of the frontal cortex is thicker than cortex at the striate area.

There is also other evidence to show that the apparent lack of effect of frontal lesions is not because the lesions were too small to produce a change of performance on the test. An investigation in progress with M. S. Rabinovitch showed that 10 cage-reared rats with small cortical lesions, not involving the striate area, had definite deterioration in performance. The size of the lesions are not yet determined exactly, but by inspection would appear to average little more than 10 per cent. (The lateral geniculates show no degeneration.) Forgays (1950) has also obtained results that parallel those previously mentioned. Studying acute transient effects of small lesions, he found no significant effect of frontal lesions and marked effects from parietal ones. However, the frontal lesions that were ineffective by themselves, when combined with parietal lesions, showed an added effect.

These two studies also indicate that small lesions outside the striate area can affect performance. The present data do not in themselves show an effect of damage to the posterior brain apart from striate damage, since the lesion size and lateral-geniculate degenaration correlate in the present study. The correlations between lesion size and lateral-geniculate degeneration are: rho = .75 for the unilateral-lesion group, rho = .66 for the posterior-lesion group.

However, further statistical analysis appeared to confirm that some of the deterioration of performance is related to damage to the posterior brain apart from striate damage. One may utilize the regression line of lateral-geniculate destruction on the error score to extrapolate to a hypothetical effect of zero destruction of the lateral geniculate. The deterioration remaining in this extrapolated error score (for zero lateral-geniculate destruction) was found to be significant (t test, 2.68; P less than .01).

A further check on some of the conclusions of this study was made by analyses of covariance. This type of analysis can be used to correct a difference on an experimental variable (e.g., error scores) for a known difference on another variable which was uncontrolled (variation in lesion size, or degeneration in lateral geniculate).

Excluding the late-posterior-lesion group from consideration because of hetergeneity of variance in test scores, the analysis

confirmed that the difference in performance between the anterior-lesion and early-posterior-lesion groups was not the result of the difference in lesion size (F, 24.0; P less than .001). Also, the effect of damaging the striate cortex was found to be similar in both the posterior and unilateral groups. The deterioration of performance apparently is a result of the lesions encroaching upon the posterior half of the cortex, irrespective of whether the damage is unilateral or bilateral.

In summary, the results of the present investigation indicate (1) no deterioration of test performance from anterior lesions; (2) a quantitative relationship between deterioration of problem-solving ability and encroachment of lesions upon the posterior half of the cortex, whether the damage is unilateral or bilateral; (3) no difference in the deterioration of performance between early- and late-lesion groups except in the bilateral-posterior group where late damage has greater effect.

DISCUSSION

In the hope of reconciling the discrepancies between the results of animal and human research on the effects of brain damage on intelligence, this investigation was designed to be more nearly analogous to the human situation. Two important features of the human data are the apparent lack of effect on intelligence by frontal lobe damage and the deleterious effects of infant lesions. Previous animal work emphasized the importance of all cortical tissue in intelligence and the slight effects of infant lesions. By using a test similar to the Binet test, and giving the experimental animals a complex environment rather than small cages to grow up in, the present investigation has obtained results different from those of previous animal work and more similar to the human data.

With the rats used in this research, no deterioration of test scores resulted from lesions in the anterior cortex. This phenomenon was shown to be a result of the locus of lesion and not the size of lesion. The effect of lesions in infancy was much greater than indicated in previous investigations.

It must be recognized that nothing can be said here about subcortical factors, independent of the cortical damage, on the basis of the results presented. This research has followed tradition in investigating the cortical factors as the first step, on the assumption that the cortex is the most important part of the brain for a consideration of intelligence.

The main problem raised by the results is to understand how lesions in the frontal area do not result in an impaired performance. Perhaps the test used here was too successful in imitating the human intelligence tests: both may have a similar blind spot for the effects of frontal lobe damage.

One possibility is that the frontal operations had two effects, one cancelling the other in the test situation so that a normal score resulted from the two abnormalities. To be more specific, there is a possibility that an anterior lesion improved motivation at the same that it decreased problem-solving "capacity"; or that something which may be called "curiosity," and which tends to increase the error score of the normal rat, was decreased, producing a more single-minded search for food by the operated rat. This might explain why brain injury in the frontal area had, apparently, no effect. It seemed that once the anterior-lesion rats found the correct solution to a problem they tended to stick to that pattern of behavior. Normal rats, on the other hand, occasionally diverge from the correct path into an error zone after having made several errorless runs. The lack of such curiosity in the rat with an anterior lesion while tending to decrease the error score could perhaps be nullified by another dysfunction tending to increase the score.

However, this would not seem to be directly relevant to the human situation, other than to suggest that deficiences expected

to lower the score on an intelligence test following frontal lobe damage might be nullified by motivational or emotional changes. Frontal lobe damage in the human is often done deliberately to relieve an individual of anxiety, depression and so on. Might the therapeutic effect of the operation compensate for other defects so as to leave the score on the general intelligence test unchanged? Some research on frontal lobe damage (reviewed in Hebb, 1950) appears to agree: premorbid IQ's may be higher than post-lobotomy IQ's, and yet pre- and post-lobotomy IQ's do not show a difference.

The present research has confirmed the earlier study done with this test (Hymovitch, 1949) which showed that the visual factor was very important in the rat's performance. Although most of the deterioration in performance appears to be related to the amount of damage to striate tissue, some extra factor also appears to be involved in the damage to the posterior cortex. Damage to tissue adjacent to the striate would appear to be of some importance (i.e., tissue not damaged by frontal lesions, but involved in unilateral and posterior lesions). Research directly on this problem is required, as such results suggest that Lashley's (1942) conception of the "autonomy of the visual cortex" may not hold for some aspects of the rat's visual perception.

Previous research that showed the rat's cortex to be equipotential in intelligence was not confirmed by this study, since

the effect of anterior and posterior lesions are so dissimilar. It may be noted that others also found a difference, not statistically reliable, between the effects of posterior lesions and anterior lesions (Lashley, 1929; Tsang, 1937). Perhaps the present test has succeeded in accurately discerning this difference.

Finally, this research has indicated that it is hazardous to assume that the tissue of one hemisphere can serve, vicariously, for any function that may be considered to be impaired by damage in the other hemisphere. The effects of unilateral and posterior lesions do not appear to differ qualitatively. The impairment appears to be largely a result of quantitative encroachment on the posterior cortex, whether the damage is unilateral or bilateral.

SUMMARY AND CONCLUSIONS

This research was concerned with the problem presented by the fact that marked differences between animal and man have been obtained in studying the effect of brain injury on intelligence. Previous rat research had demonstrated that all cortical tissue is important in intelligence, while clinical observations indicated that brain damage may not affect a patient's intelligence. Previous rat research had indicated that cortical lesions in infancy had little effect on adult behavior, while the brain-damaged child may show a declining IQ during development.

It was thought that a rat "intelligence" test more similar to the human intelligence testing technique and a more complex developmental experience for experimental rats might show results more in conformity with the human data than had previously been demonstrated. On the basis of these assumptions results were obtained showing that lesions in the anterior brain may have no effect on the rats' intelligence and that infant lesions can be almost as deleterious as adult lesions. It is concluded that these results show more similarity to the human data than previous rat investigations.

The principle that the cortex works as whole in intelligence is suggested to have serious limitations; it does not necessarily apply either to the human or rat data. It is suggested that infant brain damage in the rat may interefere with development of intelli-

gence almost as much as it does in the human.

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