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THE EFFECT OF LESIONS OF THE CINGULUM ON THE RETENTION OF VISUAL AND OLFACTORY DISCRIMINATION AND ACTIVE AND PASSIVE AVOIDANCE RESPONSES IN THE ALBINO RAT

by

Bert Mead, S. J.

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Curriculum Vitae

Bert Mead was born in Jacksonville, Florida, February 15, 1929. He graduated from Immaculate Conception High School in 1947. After attending the University of Jacksonville, he entered St. Charles College, a division of Loyola University of New Orleans and the Jesuit novitiate in the South. In 1956, he received the A. B. degree in classics from Spring Hill College, Mobile, Alabama. After teaching for three years at Jesuit High School in New Orleans, he attended St. Mary's College, the divinity school of St. Louis University, and in 1963 was granted the licentiate in theology. During the years 1965-1966, he was an instructor in philosophy at Spring Hill College, after which he was admitted to the Graduate School of Loyola University of Chicago as a doctoral candidate in psychology. From 1967 until the present he has been the research assistant of Professor Magda B. Arnold.

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CHAPTER I

INTRODUCTION

Theories of the Function of the Cingulate Gyrus

The present investigation was carried out in the light of a particular theoretical orientation which is partly a development of older theories and at the same time stands somewhat in opposition to established models. Therefore, we will begin by taking a brief look at the chief theories of the function of the cingulate gyrus, the significant limbic structure which is the object of the present study.

The Papez circuit. The first theory to suggest that a definite area of the brain is activated during the experience of emotion was proposed by the neurologist Papez in two articles published in 1937 and 1939. Papez suggested that emotions are aroused when afferent impulses arriving in the mammillary bodies ("the stream of feeling") are relayed via the anterior thalamic nucleus to the cingulate gyrus, "the seat of dynamic vigilance by which environmental experiences are endowed with an emotional consciousness (p. 737)." At the time, Morgan (1965) says, this theory "bordered on the incredulous (p. 311)." One reason why psychologists did not accept the theory, Arnold (1960a) suggests, was that it contradicted Cannon's (1927) thalamic theory of emotion without clearly showing why an excitatory theory was preferable to a theory of release from cortical inhibition. Another objection to the theory is that it cannot account for all emotions. The evidence upon which the theory was based were reports of the mental states of patients suffering from tumors which encroached on the gyrus cinguli; but as Arnold (1960a) points out, there was no evidence that fear or anxiety was caused by irritative lesions of the cingulate gyrus; and both these emotional states have been shown to be reduced by prefrontal lobotomy but not by cingulectomy, although obsessive behavior has been reduced after undercutting of the anterior cingulate gyrus. Hence, although the Papez circuit may be active in processes which may be called "affective," specific emotions have never been localized in specific cortical areas of the limbic lobe the way impressions of specific sense modalities have been localized in the primary sensory cortical areas, nor is there any indication that they ever will be.

After World War II, Smith (1945a, 1945b) found that stimulation of the rostral cingulate cortex of monkeys evoked a complex array of somatic and autonomic responses; he concluded that this

> complex response bears the connotation of emotional expression, thus definitely implicating the cingular region in the emotive process, and demonstrating the potentiality of the cerebral cortex to produce emotional expression (p. 455).

Ward (1948a, 1948b) concluded from his studies of the effects of stimulation of the anterior cingulate gyrus in monkeys that this limbic area serves two functions: it is the most powerful cortical suppressor area as well as an autonomic effector region. Both Smith (1944) and Ward (1948a) were convinced that they had observed changes in social behavior in monkeys following anterior cingulectomy, for they described the changes as loss of fear, tameness, increased curiosity, and "social indifference," all of which seemed to confirm the theory earlier proposed by Papez. However, it was not long before Pribram & Fulton (1954) published an "experimental critique" of the studies of Smith, Ward, and others. Pribram & Fulton (1954) reported that their own study of twenty cingulectomized monkeys revealed no profound or permanent behavioral changes; and so they concluded that it was too early to be certain of the functions mediated by the cingulate gyrus. While this cautionary opinion may have been a healthy antidote to the prevailing medical fashion of cingulectomy as a treatment for various psychiatric disorders, Pribram & Fulton (1954) did not investigate the precise function ascribed by Smith and Ward to the cingulate gyrus. The former investigators found that cingulectomized monkeys were unimpaired in a visual discrimination habit; but the changes in behavior noted by Smith (1944) and Ward (1948a) were not impaired visual discrimination, but loss of fear, tameness, and the behavior of walking and sitting on other monkeys which these investigators classed as "social indifference." Therefore, a behavioral deficit due to anterior cingulectomy would only be brought to light by a task which primarily involved motor activity, without additional sensory cues; for example, a delayed-response task or a right/left-alternation task. Arnold (1960a) suggested that monkeys with such lesions "would not succeed in a problem in which they would have to cooperate with another monkey, nor would they be able to avoid a tipping plank on a runway (p. 51)."

MacLean's "visceral brain". In 1949, MacLean followed Papez' lead, but he expanded the theory to include the entire limbe de l'hémisphere of Broca (1878), together with the hippocampus; he labeled the whole the "visceral brain." What had previously been named the "rhinencephalon" or the "olfactory brain," MacLean (1949) said, was "largely concerned with visceral and emotional functions (p. 351)." Because of its strategic site, MacLean (1949) wrote of the limbic lobe, it is capable of correlating all types of perception, both internal and external, by "bringing into association" various impressions from the periphery as well as from the sex organs and viscera. Because the limbic areas influence autonomic functions, MacLean (1949) thought they were the areas of the brain chiefly concerned with basic drives as well as visceral functions; and he called the limbic lobe the "visceral brain," according to Arnold (1960a),

> to distinguish it from the neocortex which controls body musculature and serves intellectual functions, and suggested that this primitive brain may serve the functions of the id, primarily concerned with oral-anal drives (p. 21).

Although many of the speculations concerning the possible function of the "visceral brain" made by MacLean (1949) should not be taken too seriously (for instance, his proposal that the hippocampal system may be capable of non-verbal symbolism), still his intriguing article drew the attention of many investigators to that part of the brain whose functions had eluded research efforts, including the hippocampal system and the cingulate gyrus. And so, although one rarely hears mention of the "visceral brain" these days, "the limbic system" is often the center of discussion when neurophysiologists and physiological psychologists meet.

McCleary's response-specificity model. After careful and systematic stimulation of the anterior limbic areas and the cingulate gyrus in cats, dogs, and monkeys, Kaada (1951) reported that stimulation of the precallosal and subcallosal gyri produced inhibition of cortically induced movements and autonomic responses; stimulation of the medial and anterior cingulate gyrus produced facilitation of these responses. Basing his hypotheses on these findings, McCleary (1961) presented evidence for a model of "response-specificity" with respect to the anterior limbic and cingulate cortex. Lesions of the septal area, McCleary (1961) found, produced a deficit in the cat's capacity to learn to stay away from food which, when touched, brought an electric shock (passive avoidance); but these lesions did not impair the learning of an active avoidance response. Lesions of the cingulate gyrus produced the opposite effect: active avoidance was disturbed, but passive avoidance was unimpaired. Previous to this report, many investigators of the conditioned avoidance response had interpreted behavioral deficits following limbic lesions as being due to interference with emotions; "but McCleary (1961) has effectively shown," insists Thompson (1967), "that such a uni-factor explanation is unlikely (p. 568)." To account for his findings, McCleary (1961) proposed that the anterior limbic cortex (including the precallosal and subcallosal areas) serves the function of inhibiting somatomotor responses, while the cingulate cortex has the function of facilitating the same responses. The "cingulate lesions" which McCleary (1961) described actually cover much more of the posterior half of the cingulate gyrus than of the anterior cingulate cortex, and, perhaps, should be called "posterior cingulate lesions." This must be taken into account when the response-specificity model is considered.

Perhaps the most telling criticism of this model is the questionable justification for equating the inhibition of cortically-induced movements in anesthetized animals with general motor inhibition. One may also ask why some responses, and not others, are inhibited or facilitated, since, theoretically, all somatomotor responses should depend on the same brain mechanism. "It is simplistic to assume," says Arnold (1969a), "that increased reactivity must be the result of a loss of 'inhibition' (p. 17)." On the other hand, septal lesions always damage the precommissural, and often the postcommissural, fornix; and cingulate ablations necessarily damage the cingulum (see Figure 1). It certainly seems likely that these, as well as other cerebral pathways and structures, are not without importance in the somatomotor activity of such complicated organisms as animals and men.

Arnold's theory of appraisal and affective memory. In 1960, Arnold proposed a general theory of the functioning of the brain as a whole which can account for the particular findings we have merely touched on here, as well as those reported more recently and to be reviewed in the third chapter. Her theory of the function of the limbic lobe may be said to be in the tradition of Papez (1937) and MacLean (1949), in that it also gives priority to the functional significance of specific circuits of the limbic system,and gives these a role in the mediation of experiences, which, although not themselves emotions, have to do with emotion and affectivity. In Arnold's formulation, the limbic areas do not form a special "visceral brain," but play a role in every psychological activity. Arnold looks upon sense experience, the appraisal of sense experience, and emotion as distinct psychological activities. Before an object, such as food, can be wanted and approached by man or animal, it has to be experienced perceptually, and then it has to be appraised as "good for me here and now." A perceived object has to be appraised as "bad for me here and now" before it can be disliked and avoided.

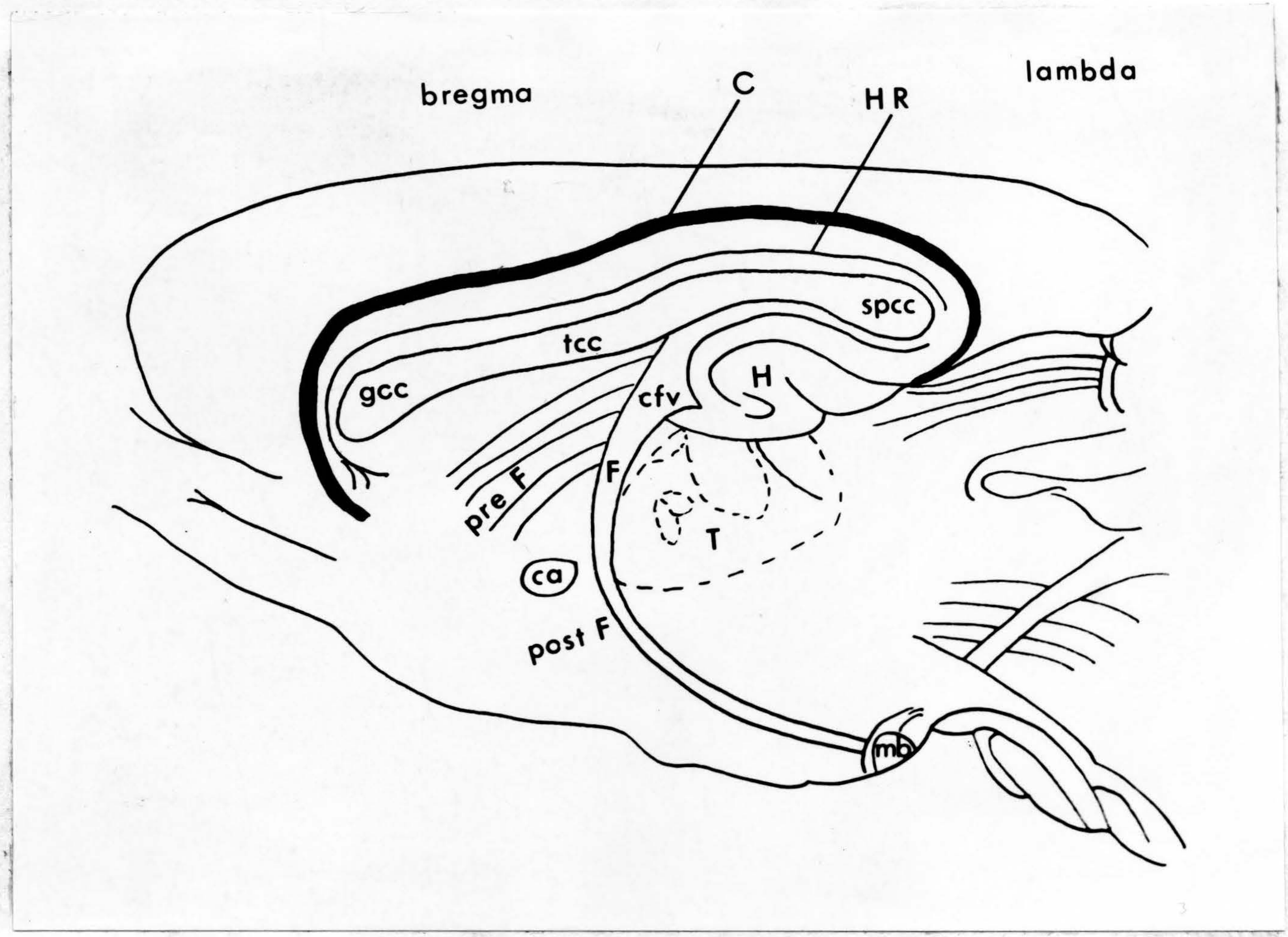

Fig. 1. Schematic diagram of the rat brain in parasagittal plane. C: cingulum; ca: anterior commissure; cfv: ventral commissure of fornix; F: fornix; pre F: precommissural fornix; post F: postcommissural fornix; gcc, tcc, spcc: genu, truncus, splenium of corpus callosum; H: hippocampus; HR: hippocampal rudiment; mb: mammillary body; T: thalamus.

An appraisal is a direct, intuitive type of value judgment of which the subject is unaware. It is not experienced as an "appraisal," just as perception is not experienced as a process: only the end-product, the thing perceived is experienced; in the same way, what is experienced when an appraisal occurs is the end-product, a positive or negative reaction to the thing appraised. Thus, appraisal forms the link between sense experience and emotion; for emotion, in Arnold's (1960b) system, is a felt tendency toward or away from something; it is produced by an appraisal, and leads to action if nothing interferes.

According to Arnold, appraisals are remembered, just as sense impressions or motor responses are remembered. But unlike sense memory and motor recall, the revived positive or negative reaction ("affective memory") is not known by the subject as a memory, but merely as a "spontaneous" positive or negative attitude toward a particular object or situation.

For Arnold, the limbic cortex, connected as it is with all sensory and motor association areas (cf. Pribram & MacLean, 1953), mediates (a) the appraisal of sense experience and movements, and (b) the revival of earlier appraisals. It should be mentioned here that Arnold considers that the prefrontal cortex serves the registration of motor responses (including speech movements, in Broca's area); and the so-called "association areas" adjacent to the primary sensory areas serve the registration of sensory patterns in the various sensory modalities. The extensive evidence from the neurophysiological literature of the past few decades, from which these inferences stem, cannot be quoted here; the interested reader is referred to Arnold's (1960a) main work. Now, to re-experience previous positive or negative reactions, a circuit is necessary which relays impulses from limbic cortex via subcortical pathways, and returns to various limbic areas (affective memory). Thus, in this system, limbic cortex mediates <u>the experience of acceptance or rejection</u>; <u>but it also mediates affective memory</u>, i.e., the spontaneous favorable or unfavorable attitude produced by an earlier beneficial or harmful experience with the same or a similar object. Without such a system which revives the <u>effects</u> of past experience, Arnold (1960a) points out, learning would be impossible, for reinforcement would be ineffective. It is not enough merely to remember a particular situation or a response to it; man or animal must also remember the effect of that situation (either harmful or beneficial), and the effect of his response (either successful or unsuccessful).

This reinstatement of past affective reactions (affective memory) is different from modality-specific registration and recall (visual, auditory, motor, olfactory, somesthetic, taste memory) and would have to be mediated by different brain structures and circuits. However, according to Arnold, both modality-specific recall and affective memory are initiated by a preliminary appraisal of the situation as "good to investigate" (via limbic cortex). This appraisal produces an impulse to (a) recall a similar earlier object or situation (modality-specific memory) and (b) to revive earlier appraisals of such situations (affective memory). Arnold suggests that the circuit mediating <u>modality-specific memory</u> runs from the anterior limbic cortex (subcallosal and cingulate gyri) <u>via the hippocampal rudiment</u> (indusium griseum), and from posterior limbic cortex (retrosplenial and hippocampal gyri) <u>via the hippocampus</u> to the precommissural fornix and brainstem, returning via the thalamic sensory and thalamic ventral nuclei to the different limbic areas. The affective memory circuit, on the other hand, runs from all limbic areas via the cingulum to the postcommissural fornix and mammillary body, and returns via the anterior thalamic nuclei to limbic cortical areas.

According to Arnold's theory, objects experienced in different modalities are appraised via the limbic cortex adjacent to the appropriate sensory association areas. Thus, the subcallosal gyrus seems to mediate the appraisal of olfactory impressions, the posterior cingulate gyrus the appraisal of somesthetic impressions, the retrosplenial and hippocampal gyri the appraisal of visual and auditory experiences; and the anterior cingulate gyrus mediates the appraisal of movements and movement impulses. Another limbic area, the insula, should connect with a similar circuit running via subcortical structures back to the insula and other limbic areas. In Arnold's theory, the anterior insula serves the appraisal of head and tongue movements, while the posterior insula mediates the appraisal of taste impressions and somesthetic impressions of the face.

Hence, we see that the Papez circuit, originally proposed as the neural substrate of emotion, has been reinterpreted by Arnold as serving functions which are psychologically prerequisite to emotion and later action; functions which are different from emotion, but are, nonetheless, intimately related to it. Moreover, Arnold has spelled out the connection of emotion with affective memory. This theory receives support from a number of investigators discussing the function of the limbic system. Kaada (1960) has written that the cingulate gyrus and the limbic system as a whole

> are concerned in higher psychic functions rather than in physiological activities of a primitive type. Data are at present accumulating which tend to show that the hippocampal-cingulate system possibly might be critically concerned in memory function (p. 1368).

Whitty & Lewin (1960) attributed the effects of eight cingulectomies in psychiatric patients to a memory loss, and explained that the regions of the brain concerned with memory seem to parallel those proposed for emotion by Papez; this, they say, should not be surprising, for "memory and emotion are indissolubly linked in normal mental life (p. 652)." Delay, Brion, Escourelle, & Marques (1961) have postulated a complex system for memory fixation, including much of the Papez circuit, based on just such evidence. Others who have concluded to a loss of a memory function following lesions of the cingulate gyrus in animals are Barker (1967), Barker & Thomas (1965), and Thompson & Langer (1963) with respect to rats; and Lubar (1964) with regard to cats. After a very lengthy review of the function of the hippocampal system in the learning process, Meissner (1966) concluded that the Papez circuit "is functionally involved in an essential process which is related to the fixing and integrating of experience in the memory bank (p. 287)." The Papez circuit is basically Arnold's (1960a) circuit for affective memory.

But affective memory is merely a revival of past "appraisals," and one may ask if this latter notion is also gradually being accepted. In a recent review, Young (1968) argued that besides the noetic and activating aspects of perception, there is also an *evaluative* aspect which "has been neglected in psychological theory but should be considered in its own right (p. 238)." In his studies of the food preferences of animals, Young (1967) insists that both cognitive appraisal and rudimentary appraisals, as Arnold

(1960a) has described them, are of fundamental importance in the study of food preferences. Pribram (1967a, 1967b) agrees that the analysis of emotion has to consider cognitive factors, and he uses the term "appraisal," although in Peters' (1965) sense, which is somewhat different from the notion proposed by Arnold (1960b).

CHAPTER II

PROBLEM

The aim of the present study is to test Arnold's notion of an "affective memory circuit" by transecting the cingulum bundle at two sites in the albino rat and testing the retention of the rats for five tasks (described in detail in Chapter IV): visual discrimination, olfactory discrimination, two-way active avoidance response (AAR), and two different tasks involving passive avoidance responses (PAR).

Site of lesion. According to Arnold's theory, relays from the various limbic areas join the affective memory circuit at different points. Hence, the site of a lesion which would interfere with particular learned performances needs considerable thought. For instance, a lesion in the anterior cingulate cortex should not disturb visual discrimination because the appraisal of something visually perceived is mediated by the affective memory circuit from the hippocampal gyrus to postcommissural fornix, mammillary body, anterior thalamic nucleus (dorsalis), and back to the retrosplenial and hippocampal gyri, a circuit unaffected by anterior cingulate lesions. The appraisal just described then produces an action impulse (an approach or avoidance tendency) via the "action circuit" running from the hippocampal gyrus via hippocampus-fornix, brainstem, ventral thalamic nuclei to frontal cortex and motor area; this circuit is also undisturbed by anterior cingulate lesions. If the situation requires approach (e.g., moving toward a cup of clear water, visually perceived and appraised as "good"), or crossing to the"safe" compartment of a shuttlebox (in AAR), the impulse to such action, mediated by the hippocampal gyrus, as described above, needs no further evaluation and can be carried out immediately. However, if the situation demands avoidance (as in a "no-go" task), the impulse to action will have to be further evaluated as inappropriate if it is to be inhibited; the anterior cingulate gyrus is required for such an appraisal, and so a lesion in this area should reveal a deficit in situations which demand the withholding of a response, such as a "no-go" situation.

Even the specific site of the cingulum lesion within the anterior cingulate gyrus is of importance. It has been suggested by Green & Adey (1956) that the cingulum fibers travel only a short distance in the cingulum before descending and penetrating the corpus callosum and reaching the thalamus. If this were the case, a combination of midcingulum (area 23) and genual lesions (area 24) should substantially increase the deficit found after one of these lesions, although each lesion should produce some interference with the appraisal of movement (see Figures 2 and 3). However, if a large portion of the cingulum fibers travel the length of the cingulum from the genu of the corpus callosum to its splenium, as can be inferred from the report of White, Nelson, & Foltz (1960), a lesion at the genu of the corpus callosum should not substantially increase such a deficit demonstrated after a midcingulum lesion. On the other hand, if the midcingulum lesion does not completely interrupt the cingulum, a second lesion at the genu of the corpus callosum, severing the cingulum either bilaterally or on the side opposite to that barely or not at all damaged by the midcingulum lesion, should produce deficits not observed after the first lesion. For

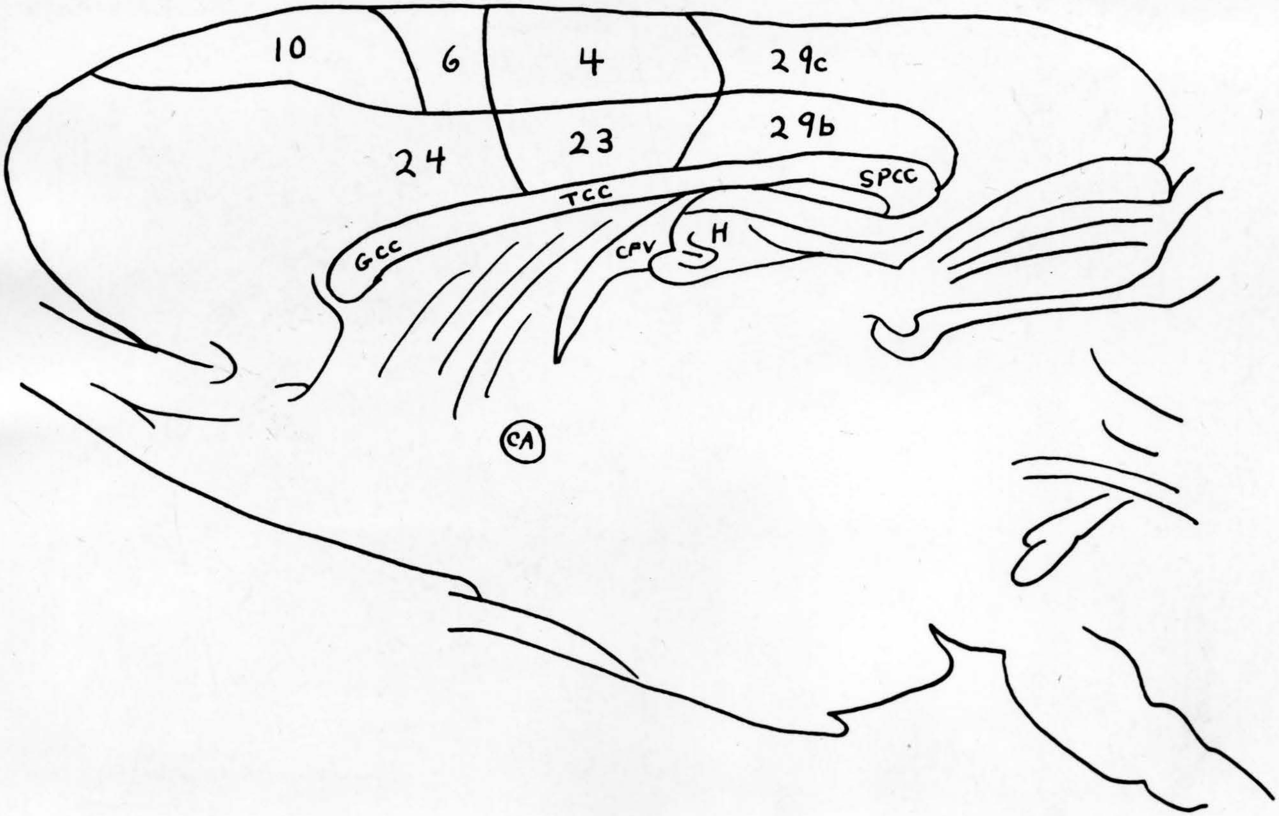

Fig. 2. Diagram of medial surface of rat brain showing Brodmann areas. CA: anterior commissure; CFV: ventral commissure of fornix; GCC, TCC, SPCC: genu, truncus, splenium of corpus callosum; H: hippocampus.

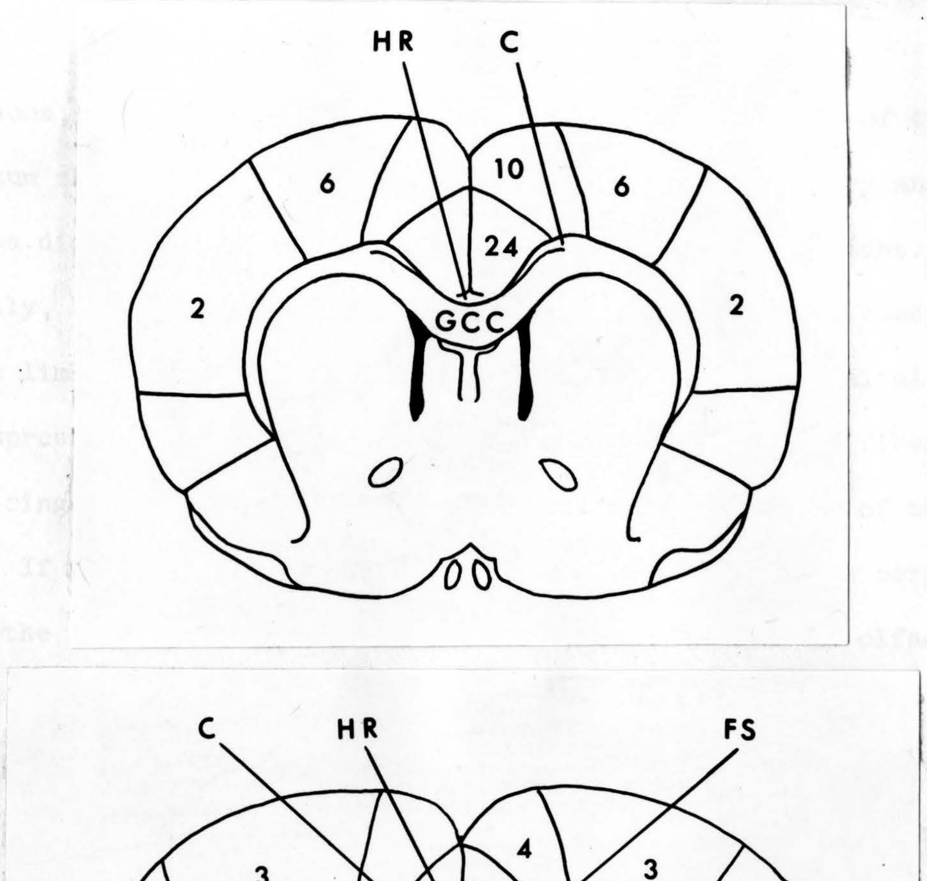

Fig. 3. Diagrams of frontal sections of rat brain at genu (top) and truncus (bottom) of corpus callosum, showing Brodmann areas. C: cingulum; cfv: ventral commissure of fornix; F: fornix; FS: fornix superior; GCC: genu of corpus callosum; HR: hippocampal rudiment.

these reasons, it was decided that a second lesion at the genu of the corpus callosum should be made in those rats in which a preliminary analysis of the data did not reveal a deficit following midcingulum lesions.

Finally, there is a possibility that some relays from the subcallosal gyrus (the limbic area, in Arnold's theory, mediating the appraisal of olfactory impressions) may travel via ascending callosoperforant fibers to the posterior cingulum instead of joining the cingulum at the genu of the corpus callosum. If that is so, neither the lesion at the genu of the corpus callosum nor the midcingulum lesion should affect retention of an olfactory discrimination task.

Tasks. Not only the lesion site, but also the tasks employed to test behavioral changes are crucial for the demonstration of a deficit in affective memory. If midcingulum and genual lesions are hypothesized to impair primarily the affective memory of appropriate or inappropriate bodily movements, tasks which demonstrate this particular deficit have to be chosen, and should be compared with tasks which show no such impairment. Since the kind of motivation might also make a difference, two "thirst-motivated" tasks and two "fear-motivated" tasks were selected. Of the former, the visual discrimination task (with only mild electric foot-shock as punishment for incorrect responses) should not be affected by the lesions; the other, the olfactory discrimination task (with unpleasant taste as punishment for incorrect responses) should not be affected, provided the relays from the olfactory appraisal area (subcallosal gyrus) do not join the cingulum bundle anterior to the genu of the corpus callosum and area 23 (midcingulum). Of the two fear-motivated tasks, two-way AAR should not be affected by either lesion, but PAR should show a retention deficit.

Two different versions of PAR were chosen to compare the effect of the lesions on a task involving hindleg-shock and a task with mouth-shock. According to Arnold, body movements are appraised as suitable or unsuitable via the anterior cingulate cortex, and head movements are appraised via the anterior insula. But, as previously mentioned, the appraisal of either movements of the body or of the head is necessary, once a task is learned, only in "no-go" situations such as PAR. This would mean that movements of the head, as in drinking, should be appraised correctly after genual and midcingulum lesions, because they depend on the intact anterior insula; but movements of the body, whose appraisal depends on both the anterior cingulate gyrus and the cingulum being intact, should not be appraised effectively; thus, PAR, which depends on the inhibition of body movements for correct performance, should show a deficit.

It should be mentioned here, for the record, that it was thought at the beginning of this investigation that the midcingulum lesion might impair the appraisal of shock to the hindlegs. According to Arnold, tactual impressions from body and hinglegs are appraised as pleasant or unpleasant via the posterior cingulate gyrus (and, perhaps, by the retrosplenial gyrus as well), and tactual impressions from the head are appraised via the posterior insula. Since area 23, the site of the midcingulum lesions of this study, is rather close to the somesthetic sensory area, in rats, damage to this area might have interfered with the appraisal of the pain of shock to the hindlegs but not shock to the mouth and head. For this reason, as well as those already given above with respect to the appraisal of movements, the two types of PAR were chosen. Both tasks required a "no-go" response as the correct response, and, therefore, both should show a deficit; but PAR with hindleg-shock would be expected to show additional impairment, if the lesion were to damage the afferent projection from the somesthetic areas. However, as the investigation proceeded, the incompleteness of information concerning the connections from somesthetic neocortex to appropriate limbic cortex in the cingulate gyrus of the rat, as well as data from other work in progress, made it seem extremely unlikely that the midcingulum lesions would damage relays from somesthetic association areas to the posterior cingulate gyrus; hence, the choice of the two different PAR tasks has little application to an hypothesis dealing with the appraisal of painful shock.

The purpose of this study. The main purpose of this investigation is to test Arnold's (1960a) theory that the anterior cingulate cortex mediates the appraisal of body movements and impulses to body movements, and that the cingulum mediates the reinstatement of past appraisals in the form of affective memory (the affective memory of body movements being mediated by the anterior cingulum, and the affective memory of somesthetic impressions being mediated by the posterior cingulum). Due to the lack of agreement among the results of previous studies of the effects of cingulate lesions on the five tasks of this study, a secondary goal will be to clarify the role of the cingulum with respect to these tasks.

Hypotheses. (1) Small, bilateral radiofrequency lesions of the cingulum at area 23 (midcingulum) in rats will (a) have no effect on the retention of visual or olfactory discrimination, two-way AAR, or PAR, mouth-shock;

(b) these lesions will impair the retention of PAR, hindleg-shock.

(2) Small, bilateral radiofrequency lesions of the cingulum at the genu of the corpus callosum (area 24) of rats, following midcingulum cingulotomy, will (a) have no effect on the retention of visual or olfactory discrimination, two-way AAR, or PAR, mouth-shock; (b) these lesions will combine with the effect of the midcingulum lesion either (i) to produce a deficit in the retention of PAR, hindleg-shock, or (ii) to make an existing deficit in the retention of the same task greater.

CHAPTER III

REVIEW OF THE LITERATURE

Since Arnold's (1960a, 1960b) main work was published, there have been many reports of the effects of cingulate lesions on the behavior of animals. McCleary's (1961) article, already referred to, touched off an explosion of research on the septal area and the cingulate gyrus. However, the chief problem in presenting an orderly review is not the quantity, but the quality, of the reports involved. There are four variable factors which are necessarily involved in a study of the effects of experimental lesions in animals, and they are more often than not combined in a different way in each separate study; these factors are: (a) species differences, (b) differences in site and magnitude of lesions, (c) differences in tasks used as behavioral measures of lesion effects, and (d) differences in the parameters of a given task. The subjects of most of the research in question have been cats and rats, which simplifies the review. But the site of the lesions were the anterior, midcingulate, or posterior regions of the cingulate gyrus, as well as the entire cingulate gyrus. In some cases the lesions were extensive ablations made by the rather crude suction method or the more refined technique of a contiguous series of electrolytic lesions, stereotaxically placed; some of the lesions were knife cuts or small electrolytic lesions. However, no matter what the site and size of the reported lesions, there is the sometimes impossible task of determining the extent of damage not only to the target structure but also to adjacent pathways and structures; the reason for this difficulty may be due to inadequate diagrams and photographs of the lesions, as well as incomplete histological descriptions of cerebral insult. For example, although there have been many reports in the last ten years of the effects of "cingulate lesions," very few of these studies have mentioned damage to the cingulum bundle; and, possibly with the single exception of Stutz & Rocklin (1968), none of the authors mentions the hippocampal rudiment which is very often transected by cingulate lesions, whether small or large, if one may judge from the published diagrams of lesions. This latter oversight is all the more strange when one thinks of the evolutionary significance of the rudiment of the hippocampus.

Even when five investigators make large "anterior cingulate" ablations in rats, one may test the lesion effects on the acquisition of a T-maze habit, another on a straight alley and PAR, a third on one-way AAR and bar-pressing, a fourth on two-way AAR and PAR, and a fifth on tasks which he designed himself but which other investigators do not use. Even if these five mythical investigators should have made the same lesions in the same species of animal and used the same behavioral tests, there might be many differences in CSs, shock levels, trial durations, etc., among these tasks.

Because of the inherent difficulty posed by these four variable factors for a meaningful review of the literature, we will procede in our review in the following manner: first, the reports will be categorized in terms of the sites of the lesions and discussed separately in the light of Arnold's theory; after this, there will be a review of the effects of cingulate lesions on behavioral tasks similar to the five tasks used in this study. There will be some overlapping, of course; but this cannot be completely avoided in a verbal description.

Neurophysiological Experiments: Evidence for or against Arnold's Theory?

Anterior cingulate gyrus. (This includes limbic areas 24, often 25 and 32; neocortical areas 4, 6, and 10; and the cingulum bundle.) It is not easy to compare the reports of the effects of "anterior limbic" or "anterior cingulate" ablations with one another, because in some cases the anterior cingulate and the precallosal limbic cortex is ablated, in others the subcallosal gyrus is damaged together with the precallosal and anterior cingulate cortex, and in some cases there are slight-to-severe invasions of the septal area through which precommissural-fornix fibers pass.

Peretz (1960) found that rats with anterior cingulate lesions learned a black/white discrimination task faster than rats with unilateral cingulate or subcallosal lesions; but this finding is not relevant since such a discrimination can be mediated by an intact thalamus; moreover, in Arnold's theory, anterior cingulate lesions leave visual affective-memory circuits intact. The same rats learned slower than rats with unilateral cingulate or subcallosal lesions to avoid shock in a one-way AAR task, and to avoid punishment in a shaking-box AAR. If the rats are not facing the "safe" compartment in a one-way AAR task, but have to turn around to look for an escape, there would be impairment, due to the inability to appraise their movements, mediated by the anterior cingulate gyrus in Arnold's theory. The same explanation applies to the shaking-box AAR, for by being shaken around, the rat loses the sense of direction it may have had before shaking commenced; and to escape, it has to find the direction of escape and what movements would bring it about. Hence, learning either of these tasks should be slightly impaired (because action impulses have to be appraised if the task is at all complicated), while retention of a "go" response need not be; for when the rat has learned to respond to the CS, as soon as the CS is seen or heard it will be appraised as "good," and this appraisal will initiate an action impulse to reach safety. Peretz' (1960) cingulectomized rats also showed a higher rate of bar-pressing for a food reward, which Peretz (1960) interprets as an "elevated response rate for food (p. 547);" but this may also be interpreted as an impairment in the ability to appraise motor performance, which could result in abnormally high or low bar-pressing rates; for if postoperatively the animal cannot appraise the effect of its movements then one would expect that bar-pressing would be unrelated to the time of reinforcement.

Cornwell (1966) found that cats with similar lesions were also defective in one-way AAR. What we have said about rats in the above study holds here, and the results can be easily explained by Arnold's theory.

Arnold would predict that anterior cingulate lesions would not interfere with learning a two-way AAR, and this has been reported for rats by Gollender (1967; however, see the discussion below concerning the lesions of his study). McCleary (1961) found that cats with similar lesions were unimpaired on the same task. Trafton (1967), however, reported that rats were impaired in learning this task. Since this investigator gives no pictorial description of his lesions, it is difficult to assess them; however, he wrote that there was "damage in subgenual area 25, and . . . large lesions in pregenual area 32 (p. 193)." It seems likely that the hippocampal rudiment was interrupted, which would impair motor recall, according to Arnold, and this would account for the obtained deficit.

With regard to the inhibition of a "no-go" passive avoidance response, which, in Arnold's theory, would be impaired by anterior cingulate lesions, Barker & Thomas (1966) reported a learning deficit in rats in a straight-alley "go no-go" situation; and Kaada, Rasmussen, & Kveim (1962) found a deficit in rats in PAR acquisition. McCleary (1961) found that cats also were impaired in learning a PAR task. Gollender (1967) reported that rats with anterior cingulate lesions were not different from normal and cortical controls in acquiring the hole-in-the-wall PAR task, which seems to disprove Arnold's theory. But, if Gollender's (1967) diagram of a single anterior cingulate lesion is typical of the group, the lack of a PAR deficit hardly argues against Arnold's theory. In this diagram, the small, stereotaxically-placed lesions are at the midline, and indicate very little damage to the anterior cingulate tissue and only a slight invasion of the most medial fibers of the cingulum.

Thompson & Langer (1963) reported a deficit in the rat's ability to learn a shock-motivated position-reversal in a T maze, following precallosal-anterior-cingulate damage, which the authors interpreted as possibly "a genuine disruption of some aspect of the memory process (p. 995);" this confirms Arnold's theory.

Barker (1967) reported that similar lesions impaired the postoperative retention of a food-motivated four-lever sequential task. He stated that "Ant. Limbic _Ss_ showed virtually no retention (p. 455)" when the correct lever was not accompanied by a visual cue, and the deficit was long lasting;

the deficit was transitory when the correct response was visually cued. This is precisely what would be expected in Arnold's theory: when the task was primarily a motor task, depending on an intact anterior cingulate gyrus and cingulum for the affective memory of appropriate movements, a deficit appeared; but when the visual cue was present to indicate the correct response, the rat associated the light with the reward following lever-pressing, appraised this as "good" via the intact hippocampal gyrus, and executed the learned task. When a simpler, two-lever, task was given to the animals to perform, the same results obtained.

Posterior cingulate gyrus. (This includes limbic areas 23 and 29; invasion of neocortical areas 4 and 7; and the cingulum.) Barker (1967) reported that, in the same two and four-lever sequential tasks (cued and non-cued) just described, rats with extensive posterior cingulate lesions were not impaired. Looking at these results from Arnold's point of view, there was no reason to expect a deficit, for the appraisal of motor behavior and the revival of the same was not interfered with, and the appraisal of somesthetic cues was not important in these tasks: there was no punishment for incorrect responses. Hence, the loss of the limbic area for appraisal and affective memory of somesthetic impressions was virtually irrelevant to the task.

Thomas & Slotnick (1963) reported that rats with bregma-to-lambda ablations (see Figure 1) acquired two-way AAR as easily as controls when they were hungry, but when they were sated a deficit appeared. The lesioned rats also had a passive avoidance deficit when they were hungry (demonstrated by spontaneous crossings in the shuttlebox), but not when sated. These findings cannot be accounted for by damage to a facilitatory system, as demanded by McCleary's response-specificity model, but they become intelligible on Arnold's (1969a) hypothesis that "the limbic cortex bordering on the somesthetic association areas mediates the appraisal of anything touched (p. 15)." Somesthetic experiences from the body and hindlegs cannot be appraised as localized pain following such an ablation. The pain will be felt (via medial thalamic nuclei) but is not associated with a particular part of the body or a concrete situation. Hence, there will be no fear of the particular place where shock was felt, and no impulse to avoid it. But the rats can still remember their response to the CS (light in the "safe" compartment), since the appropriate limbic areas are undamaged. When hungry, the lesioned rats were motivated to look for food, and so repeated their previous response of entering the lighted compartment; when satiated they were not motivated at all, for the fear drive had been eliminated by the lesion, and thus they stayed in the compartment which would normally be punishing; the authors interpreted this behavior as AAR deficit. When the rats were hungry they often crossed over to the "unsafe" compartment, which can easily be interpreted as a passive avoidance deficit, predictable by Arnold's theory.

Trafton (1967) made very similar ablations in the same laboratory in which the above study was done, and found no effect on the acquisition of the same task, in the same shuttlebox, with the same shock intensity and trial durations. As Trafton (1967) says, however, "the posterior cingulate lesioned group emitted significantly fewer CARs than the control group for the first 40 trials of CAR acquisition training (p. 195)," indicating that these animals were impaired initially. In addition, Trafton (1967) found that the animals of this group which sustained "major retrosplenial injury" came very close to a significant deficit ($p<.06$) over all trials. This evidence tends to confirm the theory of Arnold that the posterior cingulate and retrosplenial gyri mediate the appraisal and affective memory of somesthetic impressions. If the foot-shock in the shuttlebox cannot be adequately appraised, nor its past effect remembered, the animal would be impaired in AAR learning.

Barker & Thomas (1966) found that lesions very similar to those already described had no effect on a "go no-go" straight-alley alternation task, where food was available on odd-numbered trials but there was no punishment. Again, these results would be predicted by Arnold's theory, as is evident from what has been previously said.

Anterior and posterior cingulate gyrus. (This includes the cingulum; limbic areas 24, 23, 29; and invasions of neocortical areas 4, 6, 10, and 7.) The learning and retention of a straight-alley alternation in rats was impaired by these lesions, Barker & Thomas (1965) reported. This "go no-go" task was the same as that employed by these authors in 1966, described above. It seems clear that the observed deficit was due to the ablation of the anterior cingulate gyrus, with the simultaneous damage to the posterior cingulate cortex being irrelevant in this particular task.

Trafton (1967) and Kimble & Gostnell (1968) reported deficits in rats in the acquisition of two-way AAR. Since this task requires the affective memory of the pain of shock to the hindlegs and body, the ablation of the posterior half of the cingulate gyrus (to say nothing of the probable damage to the cingulum, mediating affective memory of movements and somesthetic impressions from the body) probably accounts for the deficit, at least in Arnold's theory. The same explanation applies to the reports of deficits in learning this task in cats, reported by McCleary (1961) and Lubar & Perachio (1965), with similar lesions; and the deficit in retention found by Moore (1964) may be interpreted in the same way.

The lack of a PAR learning deficit in cats, as reported by McCleary (1961), Lubar (1964), and Cornwell (1966), seems to contradict Arnold's theory, which predicts not only an impairment in a "no-go" situation when the anterior cingulate gyrus is damaged, but states that the posterior cingulate is necessary for the affective memory of painful shock. <u>However</u>, all of the cats in these three studies were shocked in the mouth. Now, affective memory on the basis of impressions from the mouth, Arnold (1969a) suggests, is mediated by the posterior insula and claustrum. Cingulate lesions would leave the memory of pain experienced in the mouth intact. Moreover, movements of the head for eating or drinking are appraised via the anterior insula in Arnold's theory, and so anterior-posterior-cingulate lesioned cats would not be incapacitated in a task which demands appraisals both of head movements and somesthetic impressions from the head.

<u>Midcingulum (area 23)</u>. The lesions of the present study are quite different from most of those surveyed thus far; the latter are extensive ablations of cingulate cortical tissue, while in this study very small lesions of the cingulum bundle were made, with much less extensive damage to cingulate cortex and the overlying neocortex. Because of this difference, a comparison of the effects of our lesions on various tasks with effects reported by other investigators has a tenuous validity. Only one published study,

that of Thomas & Slotnick (1962), reported the effects of small, midcingulum lesions of the cingulum bundle on a task used in the present study. These investigators found that interruptions of the cingulum by both knife cuts and electrolytic lesions impaired two-way AAR acquisition in rats, although there was no effect on learning an 8-cul Lashley III maze. These findings are contrary to what would be predicted by Arnold's theory. But, judging from the diagrams and histological descriptions of these lesions, it is highly probable that the knife cut spared the medial fibers of the cingulum on both sides and left the hippocampal rudiment intact; more importantly, the authors' indices of retrograde degeneration in the anteroventral and anterodorsal thalamic nuclei make it clear that the rats with the most severe bilateral degeneration made the largest number of errors. The anteroventral nucleus projects to the posterior cingulate cortex and the anterodorsal nucleus projects to the retrosplenial gyrus; in Arnold's theory these two areas mediate the appraisal of somesthetic impressions. Hence, it seems likely that the inability of these animals to appraise the pain of electric shock accounts for the deficit, and not the impairment of the affective memory of body movements alone, due to the partially interrupted cingulum. The electrolytic lesions were more posterior, in the areas of 29b and 29c; however, these lesions seem to have interrupted the hippocampal rudiment and invaded the hippocampus, while damaging only the medial and dorsomedial fibers of the cingulum; the retrograde degeneration of the anterior thalamic nuclei is substantially less in these lesions. The deficits in this group may be due to the lack of motor memory (interrupted hippocampal rudiment) as well as some impairment in the affective memory of pain; but they hardly seem due to partial severance of the cingulum. In any event, since the knife-cut experiment was conducted two years before the experiment involving the electrolytic lesions, in a different city, and in a different shuttlebox (one with scrambled polarity of grid rods, the other without it); and since the same effect was found with very different lesions; it is doubtful that this study is evidence against any theory of the function of the cingulum or the cingulate gyrus.

In an unpublished M. A. thesis, Conneely (1967) reported that electrolytic interruptions of the cingulum at area 23 produced retention deficits in rats in visual, auditory, and tactual discriminations, and T-maze single alternation; he found an improvement in olfactory discrimination. The deficit in single alternation was predictable by Arnold's theory, but the sensory-discrimination impairments appear to contradict the theory. But, Conneely's (1967) lesions extended caudally into areas 29b and 29c; therefore perhaps they are somewhat comparable to the "posterior cingulate" ablations reviewed above. Since the sensory-discrimination tasks employed by Conneely (1967) were performed in a Skinner box, with mild foot-shock as punishment, it would seem that the deficits are due chiefly to the impairment of the ability to appraise somesthetic impressions. The severance of the cingulum would also be expected to impair affective memory of movements. A secondary aim of the present study is to replicate a part of the work of Conneely (1967), and may throw some light on these difficulties.

Cingulum at the genu of the corpus callosum. There are no published studies which have made small lesions in the cingulum at this site.

Cingulum and Cingulate Lesions as they affect the Tasks of this Study

At this point we will merely outline the studies which bear on the behavioral tasks of the present study, for it would be unduly repetitious to make critical comments about them here. The page numbers showing where the following studies were reviewed above will follow each citation.

Visual discrimination. Peretz (1960) observed that rats with anterior limbic lesions were superior to operated controls in learning a black/white discrimination (p. 21). Conneely (1967) found that rats with small midcingulate lesions which bilaterally interrupted the cingulum and the hippocampal rudiment were deficient in the retention of the same visual-discrimination task of this study (p. 27).

Olfactory discrimination. Conneely (1967) reported that bilateral severance of the cingulum at area 23 (encroaching on area 29) produced improved postoperative retention in rats in the same task used in this study (p. 28).

Two-way AAR. McCleary (1961) found that anterior cingulate lesions had no effect in cats on learning this task (p. 22); Gollender (1967) reported the same for rats (p. 22). But Trafton (1967) found that such lesions interfered with learning the task in rats (p. 22).

Trafton (1967) reported that posterior cingulate lesions had no effect on AAR learning in rats (see p. 24-5 for a discussion of this); but Thomas & Slotnick (1963) found that lesions similar to Trafton's (1967) interfered with the acquisition of this task in sated rats but not in hungry rats (p. 24). The small, midcingulate lesions of Thomas & Slotnick (1962) also impaired the learning of this task in rats (p. 26).

Anterior-posterior-cingulate lesions were reported by McCleary (1961), Lubar & Perachio (1965), and Moore (1964) as interfering with learning two-way AAR in cats (p. 25). Trafton (1967) and Kimble & Gostnell (1968) reported the same for rats (p. 25).

PAR, mouth-shock. Kaada et al. (1962) reported that anterior cingulate lesions impaired the learning of this task in rats (p. 22); McCleary (1961) found the same in cats (p. 22).

With regard to anterior-posterior-cingulate lesions, McCleary (1961), Lubar (1964), and Cornwell (1966) reported that these extensive ablations had no effect on learning in cats (p. 26).

PAR, hindleg-shock. Gollender (1967) found no effect on learning in rats with anterior cingulate lesions (p. 22). Arnold (1969a) inferred from the report of Thomas & Slotnick (1963) that posterior cingulate lesions impaired passive avoidance (as defined by spontaneous crossing in the shuttlebox) in hungry rats but not in sated rats (p. 24).

CHAPTER IV

METHOD

Subjects

Twenty naive male albino rats from stock reared by Holtzman Co., Madison, Wisc., were approximately 100 days old at the beginning of the experiment and weighed approximately 250 gr. Ss were individually housed, with Rockland Rat Diet available ad-libitum. Twenty-four-hr. water deprivation was held relatively constant by giving the rats in the evening an amount which, when added to the water obtained in various testing situations, approximated 25 ml. Ss were the same in all behavioral tests; since one rat died during training and three did not survive surgery, 16 rats were tested postoperatively.

Surgery

One stage operations, using clean surgical techniques were carried out under sodium pentobarbital, injected intraperitoneally after the animal had been in a 4-l. ether chamber for 2 min. With the animal's head held fast in a Krieg-Johnson stereotaxic instrument (Stoelting Co., # 51200), two trephine holes were drilled in the skull with a # 2 round burr 1.6 mm. posterior to bregma, and 1.0 mm. lateral to the sagittal suture. A monopolar electrode, with a diameter of .075 in., insulated with Formvar except 1.25 mm. at the tip, was introduced into the brain 3.4 mm. below the surface of the skull. A Grass LM-3 radiofrequency lesionmaker delivered a current of 15 ma. for 7 sec. The wound was sprayed with antiseptic and closed with metal suture clips. Since Le Magnen (1948) has shown that penicillin and other antibiotics have a marked effect on olfactory acuity, no injections were given. After the first postoperative retention, a second lesion was made at the genu of the corpus callosum on eight rats, 1.5 mm. anterior to bregma, 5.5 mm. below the surface of the skull, and 1.4 mm. lateral to the sagittal suture.

Histology

After the experimental tasks were finished, the rats were sacrificed and perfused intracardially with isotonic saline and 10% formalin. The brains were harvested and left in 10% formalin for several weeks; then nine were imbedded in paraffin and cut at 5-μ thickness, with every 10th section stained for cellular damage with hematoxylin and eosin; and frozen sections of seven brains were cut at 30-μ thickness and stained by the Nauta technique for fibers. Histological verification revealed that following the first operation (midcingulum), 11 of the rats sustained bilateral, complete interruptions of the cingulum; these were classified as group M (see Figure 4). The five remaining rats suffered incomplete cingulotomies, and were categorized as group MI (see Figure 6).

Group M showed moderate-to-severe destruction of the cingulate cortex of area 23; in half of this group there was a slight insult to the posterior portion of area 24, and in three cases the anterior region of areas 29b and 29c was bilaterally invaded. In addition, the immediately overlying neocortex of area 4 was invaded or partially ablated in seven cases, and area 6 was slightly damaged in five cases. The corpus callosum and alveus were bilaterally penetrated in all brains, resulting in varying damage to the underlying dorsal hippocampus and fornix system. The dorsal aspect of the hippocampus was completely sectioned bilaterally in two rats; the fornix was bilaterally severed in three rats; the superior fornix and dorsal commissure of the fornix were sectioned in four rats; and the ventral commissure of the fornix was bilaterally transected in two rats (see Figure 7). The hippocampal rudiment was transected in nine rats.

Following the second operation, at the genu of the corpus callosum, it was seen that this group, labeled "G, sustained bilateral interruptions of the cingulum with slight-to-moderate damage to the anterior limbic cortex of area 24 (see Figure 5). The overlying neocortex of area 6 was invaded or ablated in six cases, and in six cases there was slight-to-moderate invasion of area 10. The corpus callosum and alveus were bilaterally penetrated in seven cases, and there was slight damage to the superior fornix in three cases. The hippocampal rudiment was severed in five cases.

Table 1 lists the histological results for each animal. Figures 4-7 show the site and coronal extent of typical lesions of the three groups.

Experimental Design

After the animals had been trained to criterion in the five tasks, they were given two weeks of rest with free access to food and water; during the last two days of this period they were deprived of water. During the retention periods, the water-deprivation schedule was such that the only water the animals received was in the tasks themselves. The preoperative and postoperative retention periods were exactly alike: 10 trials a day for each animal, in all five tasks, for five consecutive days. The sequence of tasks was as

Table 1

Summary of Histological Results for Left and Right Sides of Brain Measured on a Six Point Scale from a Minimum of 0 to a Maximum of 5 (5=interruption at the particular level)

Rat	Midcingulum lesion												
	Limbic system damage										Neocortical damage		
	Cingulum	Hipp. rudi.	Hippocampus	Fornix super.	CFD[a]	CFV[b]	Fornix	Area 23	Area 24	Area 29	Area 4	Area 6	Area 10
4	4 4	5 5	5 3	5 5	5 5	5 5	5 5	4 4	1 1	1 1	2 2	0 0	0 0
5	5 5	5 5	5 5	5 5	5 5	5 5	5 5	3 3	0 0	0 0	0 0	0 0	0 0
6	5 5	5 5	5 5	5 5	5 5	4 3	4 4	4 4	1 1	0 1	2 2	1 1	0 0
7	5 5	5 5	2 2	5 5	5 5	0 0	1 1	5 5	0 0	1 1	2 2	0 1	0 1
8	5 5	5 5	1 1	2 2	2 2	0 0	3 2	4 4	0 0	0 1	0 0	0 0	0 0
9	5 5	1 5	5 2	0 0	0 0	0 0	5 0	4 4	1 1	0 1	2 1	1 1	0 0
10	2 5	5 5	1 1	0 0	0 0	0 0	0 0	0 1	1 1	0 0	0 0	0 0	0 0
11	1 5	0 0	0 1	0 0	0 0	0 0	0 0	0 4	0 0	0 1	0 1	0 0	0 0
12	5 5	5 5	5 3	2 2	0 0	2 2	0 1	4 4	0 0	1 1	1 1	0 0	0 0
13	1 5	0 0	0 2	0 1	0 0	0 0	0 1	1 3	0 0	0 0	2 2	0 0	0 0
14	2 5	0 0	0 2	0 0	0 0	0 0	0 0	0 4	0 0	0 1	2 2	0 0	0 0
15	5 5	5 5	2 1	2 2	0 0	4 4	5 5	4 4	1 1	0 1	2 2	1 1	0 0
16	1 5	5 5	0 1	1 1	1 1	0 0	0 0	1 4	0 1	0 1	0 1	1 1	0 0
17	5 5	1 5	1 1	0 0	0 0	1 1	0 0	3 3	0 0	0 0	0 0	0 0	0 0
18	5 5	4 4	0 0	1 1	0 0	0 0	0 0	4 4	1 1	0 0	1 1	1 1	0 0
20	5 5	0 0	0 0	1 1	0 0	0 0	0 0	1 1	1 1	0 0	0 0	1 1	0 0
	Genual lesion												
4	5 4	5 5	0 0	1 1	0 0	0 0	0 0	0 0	2 2	0 0	0 0	2 2	1 1
5	5 5	1 4	0 0	1 1	0 0	0 0	0 0	0 0	2 2	0 0	0 0	2 2	1 1
6	5 5	5 5	0 0	0 0	0 0	0 0	0 0	0 0	1 1	0 0	0 0	0 0	0 0
8	5 5	4 4	0 0	0 0	0 0	0 0	0 0	0 0	2 2	0 0	0 0	2 2	0 0
10	5 5	5 5	0 0	0 0	0 0	0 0	0 0	0 0	1 1	0 0	0 0	2 2	1 1
16	5 5	5 5	0 0	2 2	0 0	0 0	0 0	0 0	1 1	0 0	0 0	1 1	2 2
17	5 5	1 4	0 0	0 0	0 0	0 0	0 0	0 0	1 1	0 0	0 0	1 1	2 2
18	3 3	0 0	0 0	0 0	0 0	0 0	0 0	0 0	1 1	0 0	0 0	0 0	2 2

[a] Dorsal commissure of fornix.

[b] Ventral commisure of fornix.

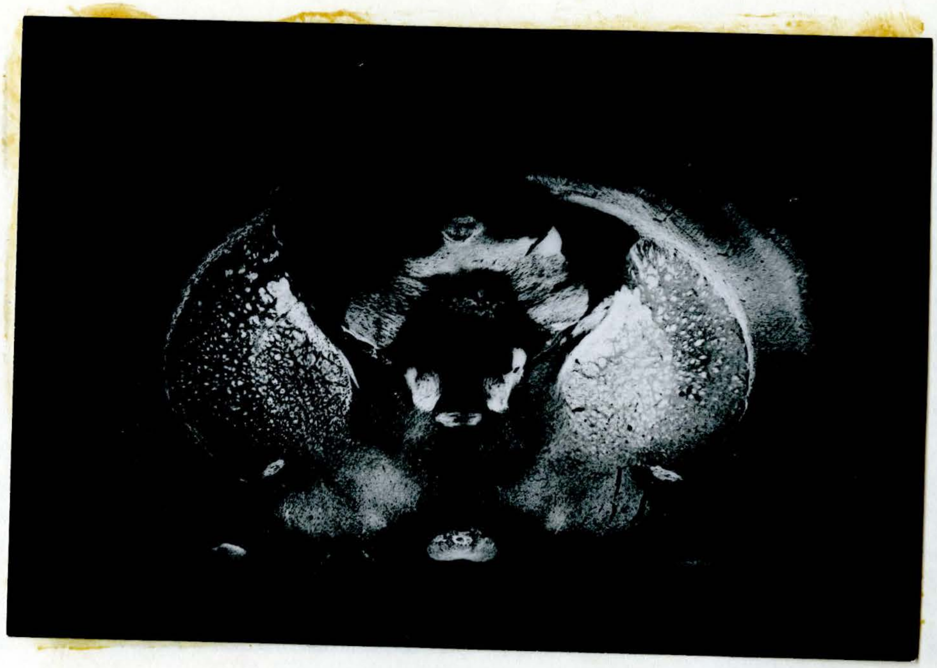

Fig. 4. Rat # 8: complete bilateral midcingulum lesion.

Fig. 5. Rat # 8: complete bilateral genual lesion.

Fig. 6. Rat # 10: incomplete midcingulum lesion.

Fig. 7. Rat # 5: midcingulum lesion with bilateral interruption of cingulum and fornix.

follows: at 8:30 a.m. the rats were weighed, after which olfactory discrimination was begun; testing in the shuttlebox (AAR) began about 9:30 a.m. At 1:00 p.m. both passive avoidance tasks were run simultaneously with different animals in each apparatus. At 7:00 p.m. the visual discrimination task ended the day's testing.

The reason for setting up the preoperative retention period in this way, namely, testing all animals in all learned tasks each day for five consecutive days, was to provide a valid and reliable method of postoperative testing of each animal on five different behavioral measures. While it was possible to train twenty rats in visual and olfactory discrimination and two-way AAR on the same days (even though each task took a different number of days to be mastered), to have also trained the same animals in two PAR tasks on these days would have been practically impossible. The olfactory and visual tasks depended on water deprivation; the rats were trained in the early morning of a particular day in olfactory discrimination, and in this task received a little water; in the late morning of the same day they were trained in the shuttlebox (no water); and at approximately 8:00 in the evening they were trained in visual discrimination, for they were thirsty again by then, which is clear from their performance. To elicit passive avoidance behavior, the approved procedure, when water is the reinforcement, is to allow the rats to drink their day's supply of water in the PAR apparatus during regular trials for several days. After the animals have become accustomed to the drinking schedule, they are intensely shocked while drinking and one may subsequently measure their ability to avoid the water. This kind of task simply would not be learned if it were interspersed with several other water-reinforcement tasks.

However, once the animals have learned five tasks, there is no reason why they may not be tested for retention of each of these tasks on the same day. In the early morning, the rat with 90% correct performance in the olfactory task will only get a little water when the correct response is drinking; it will get no more water in the shuttlebox; in the afternoon it will get no water in the two PAR tasks, because it has learned to avoid water in this situation; in the evening it will drink only during the phases of the visual discrimination task where drinking is the correct response. Now, since the testing time, sequence of tasks, and deprivation of the animals was held constant during each preoperative retention day; and since there were five days in which any possible effects of these variables could be leveled off to provide a baseline; the five-day preoperative retention period may be considered as a new learning experience for the rats. Previously, during training, the rats had learned what to do to get water and/or avoid shock, in various situations. During the preoperative retention period the rats had to learn the same thing for a particular battery of situations in a controlled sequence. There is every reason to think that by the fourth preoperative-retention day the rats had learned what to expect the day would bring when the lights were turned on in the animal room in the morning. Two weeks later (after surgery), the rats were again tested in the same sequence of tasks. If they had forgotten everything in the interval, by the fourth postoperative-retention day they should have learned what to expect and what to do, if the operation had had no effect. Thus, the preoperative and postoperative retention periods were directly comparable to one another, and the difference scores are a valid measure of the effect of the operation.

The first operation was performed shortly after the first preoperative retention period (R_1). The first postoperative retention period (R_2) followed two weeks of rest. After this retention period, half of the group received the second operation, had two weeks of rest, and then received the second postoperative retention testing (R_3).

In such a before-and-after design, where each animal is its own control, the _t_ test for the significance of the difference between dependent means is appropriate. Both individual and group scores, the latter based on the histological results, were subjected to _t_ tests, with all probabilities based on a two-tailed test of significance. With regard to the comparison of an individual rat's preoperative and postoperative scores, the mean of the scores of the 10 trials of each day was taken as the rat's score for the day in a particular task, so that the correlation between trials vanishes. Consequently, five pairs of scores were compared in each _t_ test for individual rats, with four degrees of freedom.

The experimental method and results are given below for each task separately, but the discussion of the results will be postponed to the following chapter so that the results of all tasks may be considered together for ease of comprehension.

Task 1: Visual Discrimination

Method

Apparatus. Four sound-attenuated Skinner boxes (Foringer Co. # 1102 M1) were isolated in a separate room from the electromagnetic-relay programming equipment. To control possible auditory cues, 82 db. white noise was piped into each chamber via a 2-in. Quam loud-speaker.

Procedure. Two days were allowed for shaping the rats at the beginning of training. The CS was two 4.75-w. incandescent lamps mounted above the two lever positions in the Skinner box; only the right-hand lever was in place. When these lights flashed on and off at the rate of 6 per sec., a bar-press triggered a .1-cc. dipper of water; when both lights were continuously on, a bar-press delivered a .32-ma. shock for .2 sec. through the grid floor. The quality and duration of the visual stimuli were randomly presented in consecutive daily sessions of 15 min. Each session consisted of approximately 12 trials each of positive and negative reinforcement; the duration of each trial was 22, 44, or 66 sec. The criterion was a mean of 90% correct responses for three consecutive days.

Results

Learning. Within 18 days all animals reached the criterion; the mean for the 20 animals was 12.8 days.

Retention. Analysing each rat's performance individually, it was seen that after the first operation none changed its performance significantly (see Table 2). After the second lesion, rat # 6 showed a significant deficit ($p \leq .05$) between R_2 and R_3, and an overall deficit between R_1 and R_3 ($p < .01$) in mean percent correct responses.

When the data were analysed according to histological groups (see Table 3), there was no change following either lesion with respect to correct responses or errors; however, group M pressed the bar significantly more often after the midcingulum lesion ($p < .02$). Group G attained significantly fewer

Table 2

Comparison of Mean Percent Correct Responses for Individual Rats in Retention of Visual Discrimination[a]

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
4	-3.20	8.38	-0.85	3.20	7.19	1.00	0.00	2.65	0.00
5	-4.80	7.40	-1.45	3.00	4.69	1.43	-1.80	3.42	-1.18
6	-6.00	5.10	-2.63	-13.60	9.21	-3.30*	-19.60	5.55	-7.90**
7	9.20	9.20	2.24						
8				-0.50	1.00	-1.00			
9	-1.20	1.79	-1.50						
10	0.00	2.24	0.00	-6.20	10.01	-1.38	-6.20	8.29	-1.67
11	0.80	2.75	0.54						
12	0.80	4.87	0.37						
13	-1.20	2.59	-1.04						
14	0.20	2.95	0.15						
15	0.80	3.77	0.48						
16	0.00	0.00	0.00						
17	1.20	4.32	0.62	0.80	3.56	0.50	2.00	4.47	1.00
18	5.60	6.43	1.95	-7.00	6.44	-2.43	-1.40	8.26	-0.38
20	3.80	4.87	1.74						

Note.—Rats ## 8 and 16 were withdrawn from some parts of the analysis due to performances which could not be measured.

[a] A minus sign indicates a decrement in performance.

*$p < .05$
**$p < .01$

Table 3

Group Data for Retention of Visual Discrimination[a]

Group	*N*	Bar-presses			Reinforcements			Errors			M% correct responses		
		D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
							R_2-R_1						
M	10	16.60	17.17	2.90^{**}	-0.68	5.00	-0.41	-0.66	3.53	-0.56	0.62	4.47	0.42
MI	5	7.60	6.92	2.20	3.72	4.46	1.67	0.08	0.41	0.39	-0.06	0.62	-0.19
							R_3-R_2						
G	7	3.99	14.97	0.65	0.54	2.50	0.53	3.69	6.32	1.43	-2.40	5.56	-1.14
							R_3-R_1						
G	6	4.37	11.00	0.89	-2.30	1.75	-2.93^{*}	4.83	8.33	1.30	-3.74	6.91	-1.33

Note. Rats ## 8 and 16 were withdrawn from parts of the analysis for lack of measurable performance.

[a] A minus sign indicates a decrement in performance for all measures but errors.

$^{*}p < .05$

$^{**}p < .02$

positive reinforcements after the second lesion, between R_1 and R_3 ($p<.05$).

Task 2: Olfactory Discrimination

Method

Apparatus. A narrow wooden box 15 x 4 x 8 in., painted black inside and out, with a wire-mesh ceiling-door and at one end a platform 2 1/2 in. above the floor and 2 1/2 in. from the glass end-wall, served as the test chamber. The top of the platform was a piece of Masonite painted black, which, when manually removed by *E*, signaled the beginning of a trial and uncovered a drinking cup 2 in. above the floor. The cup was a # 7 metal thimble, so filled with paraffin that it held 1.5 cc. of liquid. Ten such cups were spaced 3 in. apart and imbedded in a 1 x 2 x 12-in. board to the level of the thimble's lip. By sliding the board through a slot in the end of the box, under the Masonite cover, *E* could present one cup to the rat at a time, at a fixed position.

Procedure. Olfactory-discrimination training was administered on the same days as the visual discrimination task. No shaping was necessary. The same five cups were always used for the positive reinforcement, lemon-flavored water; the remaining five cups always contained the negative reinforcement, a vanilla-flavored quinine solution; both solutions had the same light-yellow color. The two solutions were randomly presented in 10 trials a day with an intertrial interval of 15 sec. The initial cup of a session was randomly determined. When an animal finished drinking, the Masonite cover was slipped over the top of the drinking platform, terminating the trial. The empirically-determined sign of a refusal to drink was the rat lifting its forelegs from the platform and turning away. Each session lasted about 5 min. The criterion for successful performance was a mean of 90% correct responses for three successive sessions.

Results

Learning. The criterion was reached by all animals within 20 days, with a mean of 7.25 days.

Retention. Individual results in Table 4 show that rat # 8 was significantly inferior in mean percent correct responses following the midcingulum lesion ($p<.05$), but performed better than the preoperative level following the second lesion, so that the change from R_2 to R_3 showed a very significant improvement ($p<.01$).

Analysis of histological groups revealed no significant changes with respect to correct responses (see Table 5). But group M had significantly shorter latencies following the midcingulate lesion ($p<.01$); after the genu lesion, group G showed an overall (R_1 to R_3) decrease in latencies ($p<.05$).

Task 3: Active Avoidance Response

Method

Apparatus. A double-grill shuttlebox (Lafayette Instrument Co. A-580) 24 x 8 x 8 in. with stainless steel walls except for a one-way mirror on one side was used for two-way AAR learning and retention. The two compartments, each illuminated by an 8-w. fluorescent lamp shining through a white plastic ceiling-door were divided by an unpainted Masonite partition with a central opening 6 in. high, 5 in. wide at the base, and tapering to 2 in.

Table 4

Comparison of Mean Percent Correct Responses for Individual Rats in Retention of Olfactory Discrimination[a]

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
4	4.00	15.17	0.59	0.00	0.00	0.00	4.00	15.17	0.59
5	-10.00	12.25	-1.83	2.00	14.83	0.30	-8.00	17.89	-1.00
6	2.00	10.95	0.41	0.00	0.00	0.00	2.00	10.95	0.41
7	2.00	4.47	1.00						
8	-18.00	13.04	-3.09*	22.00	8.37	5.88**	4.00	11.40	0.78
9	2.00	4.47	1.00						
10	2.00	4.47	1.00	-4.00	5.48	-1.63	-2.00	4.47	-1.00
11	2.00	8.37	0.54						
12	4.00	5.48	1.63						
13									
14	-4.00	5.48	-1.63						
15	-2.00	4.47	-1.00						
16	-4.00	5.48	-1.63	2.00	8.37	0.54	-2.00	8.37	-0.54
17	8.00	8.37	2.14	-2.00	4.47	-1.00	6.00	8.94	1.50
18	4.00	5.48	1.63	0.00	0.00	0.00	4.00	5.48	1.63
20	2.00	4.47	1.00						

Note.—Rat # 13 was withdrawn from the analysis due to lack of performance on several days.

[a] Minus sign indicates a decrement.

*$p < .05$

**$p < .01$

Table 5

Group Data for Retention of Olfactory Discrimination[a]

Group	N	M % correct responses			Response latencies		
		D_M	SD	t	D_M	SD	t
R_2-R_1							
M	11	-0.18	7.11	-0.08	-0.67	0.56	-3.75**
MI	4	-1.00	3.00	-0.58	-0.52	0.37	-2.42
R_3-R_2							
G	8	2.50	7.60	0.87	-0.22	0.63	-0.93
R_3-R_1							
G	8	1.00	4.36	0.61	-0.97	0.90	-2.86*

[a] A minus sign for correct responses is a decrement; for latencies it indicates improvement.

*$p < .05$

**$p < .001$

wide at the top. This partition could be raised or lowered, but the threshold was usually kept 1/2 in. above the grid floor. A shock from .60 to 2.50 ma. could be given through the grid floors, with polarity scrambled by a Lafayette A-620 grid scrambler.

Procedure. Avoidance training was begun in a semi-dark room 16 days after visual and olfactory discrimination training was finished, with 10 trials on the first day and 20 trials each day thereafter. The ceiling-light of the shuttlebox was the CS. To begin each session, the rat was placed in the randomly determined illumined compartment. When the light went off in this compartment, it came on immediately in the other, and the animal had 5 sec. to leave the dark compartment before its grid floor was charged; this grid remained charged until the next light change. The intertrial intervals were of 15, 30, and 45 sec. duration, and were randomly ordered. Five different responses were visually ascertained by E: (1) escape (after shock), (2) avoidance (arrival in the illumined compartment within 5 sec. after the CS), (3) non-crossing (when the grid became charged, the rat either remained in one position throughout the trial or scurried around in the dark compartment), (4) spontaneous crossing (entering the dark compartment where the grid was charged), and (5) near-avoidance (when the rat's forelegs were in the illumined compartment, but its hindlegs received shock as the animal crossed the threshold). Avoidance (2) was the only correct response. To eliminate non-crossing (3) during training sessions (but not during retention sessions), E opened the ceiling-door after a rat had spent a significant length of time enduring shock, and stimulated it with an electrically-charged prod; this was partially successful in eliciting escape behavior from a few animals in subsequent trials. The criterion of successful learning was a mean of 85% avoidances on three successive days. To eliminate auditory cues, extraneous sounds were kept erratic by the playing of a disc-jockey radio program during all sessions.

During the learning trials, it was soon apparent that some changes were in order for the apparatus; hence, the following adaptations were made for the retention periods: since the animals often perched on the threshold of the partition between the two compartments, the Masonite partition was replaced by an unpainted 1/4-in. plywood partition with a door 4 1/2 in. high and 3 1/2 in. wide, with # 14 copper wire arranged on the threshold (which was 1/2 in. above the level of the grid floor) in such a way that it could be electrically charged. The fluorescent ceiling lights were replaced by 25-w. incandescent lamps. The shock-level of the grid floor and threshold was maintained at 1.0 ma.

Results

Learning. Training was terminated after 28 days, since it was evident that the animals which had not reached the demanding criterion had little probability of success. Ten rats met the criterion in a mean of 9.9 days.

Retention. Animals ## 7 and 20 made significantly more errors after the first lesion (both $p < .05$; see Table 6).

The group data revealed no significant effect of either operation with respect to avoidances, near avoidances, spontaneous crossings, or total errors (see Table 7). Because of the changes in the apparatus after training, R_1 could be viewed as a learning situation instead of a preoperative retention period. But when the data were analysed from the point of view of error-savings, no significant changes were noted.

Task 4: Passive Avoidance Response, Mouth-Shock

Method

Apparatus. An unpainted 1/2-in. plywood box, 10 x 10 x 8 in. with a wire-mesh floor and a plywood ceiling-door (to which an 8-w. fluorescent lamp was attached) was patterned after McCleary's (1961) apparatus for the cat. A small 2 x 3 1/4 x 2 1/2-in. chamber, 4 in. above the floor was built into one of the corners; it was separated from the larger compartment by a Masonite guillotine door, which E manually operated as a signal for the onset and end of a trial. The wooden floor of the smaller chamber was covered with wire-screen except for a hole in the center where a # 7 insulated metal thimble, holding 2.7 ml. of liquid, was half-imbedded in a hole bored into the wooden floor. This cup was the positive pole, the wire-screen the negative pole, of a potential 2.5-ma. circuit. A toggle switch made it possible to have the current continuously "on" or "off." The rear wall of the small chamber was a one-way mirror, removable in order to replenish the water in the cup by means of a hypodermic syringe. Eighty-two db. white noise was piped into the experimental room via a 5-in. loud-speaker mounted on the wall.

Procedure. Sixteen days after the shuttlebox task was ended, training began. Since rat # 19 had expired in the interval, the N was reduced to 19. When a rat stood on its hindlegs with its forelegs resting on the wire-screen-covered floor of the 4-in. high chamber, it could easily drink from the cup; when the current was turned on, such behavior completed the circuit, deliver-

Table 6

Comparisons of Total Errors of Individual Rats in Retention of Active Avoidance Response[a]

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
4	-0.20	1.10	-0.41	0.00	0.71	0.00	-0.20	0.84	-0.54
5	-1.00	2.45	-0.91	0.40	0.89	1.00	-0.60	2.70	-0.50
6	-1.40	2.51	-1.25	0.20	1.92	0.23	-1.20	1.30	-2.06
7	2.60	2.07	2.80*						
8	-0.60	1.14	-1.18	-0.80	1.48	-1.21	-1.40	1.52	-2.06
9									
10	-0.20	1.30	-0.34	2.40	3.65	1.47	2.20	3.77	1.30
11	1.60	2.07	1.72						
12	0.80	1.48	1.21						
13	0.60	1.67	0.80						
14									
15	0.00	1.58	0.00						
16	-0.60	1.82	-0.74	0.20	1.10	0.41	-0.41	1.14	-0.78
17	-0.60	1.67	-0.80	-0.20	1.64	-0.27	-0.80	3.27	-0.55
18	-0.20	1.10	-0.41	-0.20	0.84	-0.54	-0.40	1.14	-0.78
20	2.00	1.58	2.83*						

Note. Rats ## 9 and 14 were withdrawn from the analysis because they had not acquired the AAR habit.

[a] A minus sign indicates an improvement.

*$p < .05$

Table 7

Group Data for Retention of Active Avoidance Response[a]

Group	*N*	Avoidances			Near avoidances			Spontaneous crossings			Total errors		
		D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
R_2-R_1													
M	10	-0.40	11.99	-0.10	0.50	1.12	1.34	0.50	1.20	1.25	0.70	6.12	0.34
MI	4	-3.50	8.41	-0.72	1.50	2.69	0.96	-0.25	0.43	-1.00	1.75	4.21	0.72
R_3-R_2													
G	8	0.25	5.70	0.12	0.38	1.32	0.75	1.00	2.65	1.00	1.38	4.72	0.77
R_3-R_1													
G	8	7.00	8.25	2.25	0.25	0.97	0.68	1.38	2.40	1.52	-1.63	5.50	-0.78

Note.—Rats ## 9 and 14 were withdrawn from the analysis because they failed to acquire the AAR habit.

[a] A minus sign indicates a decrement in performance for "avoidances," but an improvement for the other measures.

ing a shock to the rat's mouth. The intertrial interval was 30 sec., and each trial lasted 30 sec. The task lasted six consecutive days. During 10 trials of the first three days, the animal was allowed to drink freely from the cup in the elevated chamber; this was its only source of water for the day. On Day 4, the first two trials were the same as previously, but on the third and all subsequent trials, the current was turned on throughout the trial. When a rat avoided the cup for 10 consecutive trials, after shock, it was returned to its home cage; otherwise, it was kept in the test situation until 20 trials (inclusive of the first two non-shock trials) were completed. On Day 5, the animal was given 10 "free" trials, i.e., with the current continuously "off." On Day 6, the current was "on" only during the first trial of ten trials.

The rats' behavior during acquisition indicated that two decisions had to be made with regard to the retention periods: (a) the current would be kept continuously "on" during all retention trials, and (b) the animals would be scored for the number of "complete approaches" made during a trial. This form of behavior was noticed in several rats during learning trials, on Days 5 and 6. When the guillotine door was raised, these animals often poked their heads into the small chamber containing the water, then withdrew quickly. A "complete approach" was defined thusly: when the rat, standing on its hindlegs, placed its forelegs on the wire-screen and held its mouth a few millimeters above the cup without actually touching the cup.

Results

Learning. Eighteen of the 19 rats made 10 consecutive avoidances after shock on the first shock day, Day 4. On Day 5, eight rats made 10 consecutive avoidances; the remaining 11 rats had a mean of 2 avoidances. On Day 6, six rats made 10 consecutive avoidances, four made nine, and the remaining nine had a mean of 3.5.

Retention. None of the 16 surviving rats changed their preoperative retention patterns of near-perfect avoidance following the two operations (see Table 8). Rats ## 15 and 17 made significantly more complete approaches after the midcingulum lesion ($p<.02$ and $p<.05$, respectively); rats ## 4 and 18 showed a significant increase between R_2 and R_3 ($p<.02$ and $p<.01$), and ## 4, 8, and 18 showed a significant overall increase from R_1 to R_3 following the lesion at the genu of the corpus callosum ($p<.05$, $p<.02$, $p<.05$; see Table 9).

The M group made significantly fewer errors ($p<.05$) but more complete approaches ($p<.05$) following the first operation; group G made significantly more complete approaches overall from R_1 to R_3 ($p<.02$; see Table 10).

Task 5: Passive Avoidance Response, Hindleg-Shock

Method

Apparatus. A modified Skinner box, in a sound-attenuated chamber (Foringer Co. # 1102 Ml) was used. The response panel was replaced by a one-way mirror, and a # 7 metal thimble (2.7 ml.) was soldered to the dipper mechanism. When the dipper was in the drinking position, a 1/4-in. plywood crescent-shaped 2 x 1-in. platform taped to the last grid rod surrounded it. The four rods nearest the dipper were wrapped in electrical tape for a length of 4 in. in the center of the grid. The sides of the metal chamber were diagonally striped with a 1-in. white strip of tape at 1-in. intervals. An external 25-w. incandescent lamp provided illumination for the interior of the

Table 8

Comparisons of Errors of Individual Rats in Retention of Passive Avoidance Response: Mouth-Shock

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	t	D_M	SD	t	D_M	SD	t
4	0.00	0.00	0.00	0.80	1.17	1.38	0.80	1.17	1.38
5	-0.20	0.40	-1.00	0.20	0.40	1.00	0.00	0.00	0.00
6	0.00	0.00	0.00	2.00	2.61	1.54	2.00	2.61	1.54
7	0.00	0.00	0.00						
8	-0.20	0.40	-1.00	-0.20	0.40	-1.00	-0.40	0.80	-1.00
9	0.00	0.00	0.00						
10	0.00	0.00	0.00	-0.20	0.40	-1.00	-0.20	0.40	-1.00
11	0.00	0.00	0.00						
12	-0.20	0.40	-1.00						
13	0.00	0.00	0.00						
14	0.00	0.00	0.00						
15	0.00	0.63	0.00						
16	0.00	0.00	0.00	0.20	0.40	1.00	0.20	0.40	1.00
17	0.00	0.00	0.00	0.60	0.49	2.45	0.60	0.49	2.45
18	-0.20	0.40	-1.00	0.20	0.40	1.00	0.00	0.00	0.00
20	0.00	0.00	0.00						

[a] A minus sign indicates improvement.

Table 9

Comparisons of Complete Approaches of Individual Rats in Retention of Passive Avoidance Response: Mouth-Shock[a]

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
4	0.40	0.89	1.00	5.80	3.35	3.88**	6.20	4.02	3.44*
5	0.40	0.55	1.63	0.40	0.89	1.00	0.80	0.84	2.14
6	1.80	2.59	1.56	0.60	3.21	0.42	2.40	2.70	1.99
7	0.80	0.84	2.14						
8	0.00	1.58	0.00	0.80	1.30	1.37	0.80	0.45	4.00**
9	0.60	0.89	1.50						
10	0.20	0.45	1.00	0.20	0.45	1.00	0.40	0.55	1.63
11	-0.40	0.89	-1.00						
12	0.00	0.00	0.00						
13	0.00	0.00	0.00						
14	0.00	0.00	0.00						
15	2.80	1.64	3.81**						
16	0.00	0.00	0.00	0.40	0.55	1.63	0.40	0.55	1.63
17	4.60	2.97	3.47*	-2.00	4.06	-1.10	2.60	3.05	1.91
18	1.00	2.65	0.85	2.80	1.10	5.72***	3.80	2.39	3.56*
20	-0.20	0.45	-1.00						

[a] A minus sign indicates a decrement in this behavior.

* $p < .05$

** $p < .02$

*** $p < .01$

Table 10

Group Data for Retention of Two Passive Avoidance Response Tasks[a]

Group	N	PAR: mouth-shock						PAR: hindleg-shock					
		Errors			Complete approaches			Errors			Complete approaches		
		D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*	D_M	SD	*t*
							R_2-R_1						
M	11	-0.36	0.48	-2.39*	5.54	6.92	2.53*	1.18	3.95	0.95	10.73	7.79	4.35***
MI	5	0.00	0.00	0.00	-0.14	0.83	-0.42	-0.80	0.75	-2.14	4.00	6.07	1.32
							R_3-R_2						
G	8	2.25	3.35	1.78	5.62	10.71	1.39	3.75	2.95	3.37**	-1.88	10.62	-0.47
							R_3-R_1						
G	8	1.88	3.59	1.38	10.88	9.55	3.01**	3.50	2.18	4.25***	6.00	6.42	2.47*

[a] A minus sign with errors indicates improvement, with complete approaches a PAR decrement.

*$p<.05$

**$p<.02$

***$p<.01$

chamber through the ceiling observation-window of the outer case. Eighty-two db. white noise was piped into the box via a 2-in. Quam loud-speaker. E could observe the rat through a plexiglass-covered circular opening 3 in. in diameter at the rear of the sound-attenuating case, and thence through the one-way mirror which was the rear wall of the test-chamber itself. A 2.5-ma. current delivered through the grid floor was controlled by a button-switch operated by E when an animal was observed to drink from the cup. During the retention periods, a 2 1/2 x 10 x 1/4-in. Masonite platform was attached to the last three grid rods, those farthest from the water, upon which the rat was able to crouch when passively avoiding shock. This was only added after training was over, however; it was found to be necessary due to the fact that a very mild induction current momentarily charges the grid of this test-chamber when the motor operating the dipper mechanism is activated. During training the rats did not seem to be bothered by this slight tingle of shock, but postoperatively they appeared to be very sensitive to it.

Procedure. Five days after the passive avoidance task in which shock was given to the mouth, the PAR task with hindleg-shock was begun. During the 10 trials of the first 4 days, the animals were allowed to drink freely from the cup for 30 sec., with an intertrial interval of 30 sec. This was the only source of water for the rats on these days. On Day 5, the first two trials were the same as previously, but on all subsequent trials until the end of the experiment, the rats were shocked whenever they began to drink. After a rat had avoided the water for 10 trials in a row, after receiving shock, it was returned to its home cage; otherwise, it remained in the test situation until a total of 20 trials was completed. On Days 6 and 7, each animal had 10 trials, and was shocked whenever it began to drink. Days 8 and 9 were added for those animals which had not attained 10 consecutive avoidances.

A "complete approach" was defined as the behavior in which a rat placed its forepaws on the insulated platform surrounding the raised cup of water and held its head a few millimeters above the water without drinking, its hindlegs touching the uninsulated grid rods, and then quickly withdrawing.

Results

Learning. Thirteen rats met the criterion on the first shock-day, Day 5. On Day 6, three rats made 10 consecutive avoidances, seven made nine out of 10, and the rest had a mean of 6.7 avoidances. On Day 8, three rats which had not made 10 in a row succeeded, and on Day 9, two more succeeded.

Retention. From the individual results of Table 11 it appears that rat # 15 made significantly more errors after the first operation ($p<.05$), and ## 17 and 18 made significantly more after the second, when R_2 and R_3 were compared ($p<.02$). Rats ## 4, 7, 18, and 20 made significantly more complete approaches after the midcingulum lesion ($p<.01$, $p<.05$, $p<.05$, $p<.001$, respectively; see Table 12). Following the second lesion, # 4 made significantly fewer complete approaches, when R_2 and R_3 were compared ($p<.05$), and # 18 made significantly more overall (R_1 and R_3), $p<.05$.

Table 10 shows that the effect of the first lesion on group M was a significant increase in complete approaches ($p<.01$). The effect of the second lesion was a significant increase in errors from R_2 to R_3 for group G ($p<.02$), and from R_1 to R_3 ($p<.01$); in addition, group G showed an overall increase in complete approaches ($p < .05$).

Table 11

Comparisons of Errors of Individual Rats in Retention of Passive Avoidance Response: Hindleg-Shock[a]

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	t	D_M	SD	t	D_M	SD	t
4	0.00	0.71	0.00	0.40	1.14	0.78	0.40	0.55	1.63
5	0.40	0.89	1.00	0.40	1.82	0.49	0.80	1.30	1.37
6	-0.40	0.55	-1.63	1.80	2.39	1.69	1.40	2.07	1.51
7	0.20	0.45	1.00						
8	0.20	0.45	1.00	0.00	0.71	0.00	0.20	0.45	1.00
9	-0.20	0.45	-1.00						
10	0.00	0.00	0.00	0.40	0.55	1.63	0.40	0.55	1.63
11	-0.20	0.45	-1.00						
12	-0.20	0.45	-1.00						
13	0.00	0.00	0.00						
14	-0.20	1.92	-0.23						
15	1.80	1.30	3.09*						
16	-0.40	0.89	-1.00	0.60	1.34	1.00	0.20	0.45	1.00
17	-0.40	0.89	-1.00	1.60	0.89	4.00**	1.20	1.48	1.81
18	0.20	1.30	0.34	0.80	0.45	4.00**	1.00	1.00	2.24
20	0.20	1.48	0.30						

[a] A minus sign indicates an improvement.

*$p < .05$

**$p < .02$

Table 12

Comparisons of Complete Approaches of Individual Rats in Retention of Passive Avoidance Response: Hindleg-Shock[a]

Rat	R_2-R_1			R_3-R_2			R_3-R_1		
	D_M	SD	t	D_M	SD	t	D_M	SD	t
4	4.80	1.79	6.00**	-4.00	2.83	-3.16*	0.80	1.79	1.00
5	0.20	0.45	1.00	-0.20	1.64	-0.27	0.00	1.73	0.00
6	1.00	1.22	1.83	0.40	1.82	0.49	1.40	2.88	1.09
7	2.20	1.64	2.99*						
8	2.40	3.36	1.60	-2.00	3.54	-1.26	0.40	0.55	1.63
9	0.20	0.45	1.00						
10	0.00	0.00	0.00	4.00	4.24	2.11	4.00	4.24	2.11
11	0.00	1.87	0.00						
12	1.60	2.61	1.37						
13	0.40	0.55	1.63						
14	3.20	5.07	1.41						
15	3.00	3.54	1.90						
16	0.40	2.19	0.41	-0.20	1.79	-0.25	0.20	1.48	0.30
17	0.40	1.52	0.59	0.00	1.87	0.00	0.40	1.14	0.78
18	3.40	2.70	2.81*	-1.00	1.41	-1.58	2.40	1.67	3.21*
20	4.40	0.89	11.00***						

[a] A minus sign indicates a decrement in this behavior.

*$p<.05$

**$p<.01$

***$p<.001$

CHAPTER V

DISCUSSION AND CONCLUSIONS

Visual discrimination. The hypothesis that neither the midcingulum nor the genual lesion would impair visual discrimination was confirmed, since there was no significant change in a sufficient number of animals nor in the various groups, following either lesion.

Only rat # 6 performed significantly worse after the second lesion; in this animal the dorsal hippocampus, superior fornix, and dorsal commissure of the fornix were bilaterally severed, and there was severe damage to the fornix and ventral commissure of the fornix. Hence, it is possible that the deficit is due to the damage to these structures, which are part of the modality-specific and affective memory circuits, as well as the "action circuit," in Arnold's thory. Moreover, lesions of the hippocampus or fornix have been found to impair the retention of a visual-discrimination task (see Arnold, 1969b). This suggestion is supported by the fact that rats ## 4 and 5, with comparable damage to the hippocampal-fornix fibers, were slightly deficient in this task.

None of the groups changed significantly in visual discrimination after either operation, except that group M pressed the bar significantly more often after the midcingulum lesion, and group G pressed the bar significantly less during the positive phases of the program, after the second lesion. This does not indicate an impairment of visual discrimination, for percentages of correct and incorrect responses were not affected; because of the nature of the programming equipment employed, it was possible for an animal to press the bar several times but obtain only one positive reinforcement. What it does indicate is that the animals were no longer able to gauge the appropriateness of bar-pressing; that is, their affective memory for success or appropriateness of their movements was impaired. This was not anticipated before the data were analyzed, but could have been predicted on the basis of Arnold's theory: since in both lesions the appraisal area for movement was damaged, every performance skill should be impaired to some extent.

Conneely's (1967) findings are comparable to the present study, for his lesions also interrupted both the cingulum and the hippocampal rudiment at area 23. He reported a significant deficit in retention of the same visual task of this study. But his lesions averaged 4.5 mm. in the parasagittal plane, while the lesions in our study had a mean length of 2.9 mm.; more importantly, his lesions invaded areas 29b and 29c for the length of a millimeter posterior to the junction of areas 23 and 29, whereas the caudal termination of the lesions of this study was immediately posterior to this junction, with only slight encroachments on areas 29b and 29c in three brains. Therefore, Conneely's (1967) lesions ablated substantially more of the posterior cingulate cortex than those of the present study. As explained in Chapter I, the posterior cingulate and the retrosplenial gyri have been suggested by Arnold (1960a) as the areas which mediate the appraisal of somesthetic impressions. Now, Conneely (1967) found retention deficits in all sensory discrimination tasks which were performed in the Skinner box, where shock to the feet is the punishment. If the rat is impaired in its capacity to evaluate this shock, and cannot readily recall how pain affected it in the past, then no matter what the sense modality involved in the discrimination task, it should have a difficult time performing. If, on top of this, the anterior cingulum and hippocampal rudiment are interrupted, the affective memory of what movements were successful or unsuccessful in the past, as well as simple motor recall of what patterns made up successful movement, would be disturbed, and one would predict the deficits found. This interpretation makes understandable many of the reported deficits in two-way AAR following posterior cingulate lesions; but this will be taken up below in its proper place.

Olfactory discrimination. The hypothesis that olfactory discrimination would not be impaired by either or both of the lesions of this study was confirmed. Only rat # 8 made significantly more errors after the first lesion in this task; but after the second, the same rat significantly improved beyond the first preoperative level, which seems to indicate that the poor performance in the first postoperative retention period (R_2) may have been due to some extrinsic influence such as a respiratory condition. When we consider olfactory response latencies we see that only rats ## 8 and 18 had longer latencies after the first operation.

Group comparison reveals that after both operations the groups retained the olfactory habit but performed it significantly faster. Conneely (1967) reported that rats with the same lesions improved in retention of the same task; however, two studies conducted in the Behavior Laboratory of Loyola University of Chicago, which are being prepared for publication (Arnold & Mead, 1969; Arnold, 1969b), show that rats with very similar lesions had a learning deficit in the very same task. The reason learning this task was impaired but not retention, is probably due to the fact that learning any task which depends on the appraisal of movements of the body would be impaired if the pathway in the brain mediating such appraisal were interrupted. In the olfactory task of this study, the test box is so narrow that the rat cannot turn completely around in it without rearing on its hindlegs, touching the walls of the box, and turning and resting on all fours. Now, very often when a rat has tasted the punishing quinine solution it turns around and faces the rear wall; and on the next trial it has to turn completely around to face the other end of the box. If the rat cannot appraise its movements correctly, it would fail to learn this task. Once the task has been normally acquired, however, the visual cues and unimpaired appraisal of taste impressions and head movements (intact insula) should be enough to ensure correct performance of the habit.

Two-way AAR. The hypothesis of no effect in this task was confirmed. Only two of the rats, ## 7 and 20, showed a significant AAR retention deficit, and that following the midcingulum lesion. Both of these animals sustained complete bilateral cingulotomies; # 20's hippocampal rudiment was intact, but the rudiment of # 7 was severed; in rat # 20 there was minimal damage to area 23 and no involvement of area29, while # 7 suffered the greatest loss in area 23 of any rat as well as moderate invasion of area 29, and this to a degree sustained by only two other animals. Hence, the deficit observed in # 7 could be interpreted as due to a lack of the ability to remember past affective reactions to somesthetic impressions, due to the damage to the posterior cingulate gyrus; a lack of motor memory, due to the interruption of the hippocampal rudiment; and a lack of affective memory of body movements, due to interruption of the cingulum. But it is difficult to understand why rat # 20 also had a deficit. If one could validly test a theory on the basis of one case, the performance of rat # 20 on two-way AAR would be evidence against Arnold's theory that this task should not be impaired by cingulum interruption.

There was no group effect in the two-way AAR task. This confirms the finding in the study of Arnold & Mead (1960) that similar lesions in rats had no effect on learning this task; but it is contrary to the later finding in the same laboratory (Arnold, 1969b) that learning a two-way AAR was significantly impaired by bilateral interruptions of the cingulum and hippocampal rudiment at the same site. The latter study made some changes in the shuttlebox task: there were only five trials a day for ten days. In the Arnold & Mead (1969) task there were twenty trials a day until 85% correct responses were recorded for three consecutive days. This difference in design may account for the discrepancy, in that the Arnold & Mead (1969) task was easier to learn than the Arnold (1969b) task.

Indirect support for the findings of this study comes from the investigations of the effects of cingulectomy on learning two-way AAR by Thomas & Slotnick (1963) and Trafton (1967) with rats as <u>Ss</u>; for they all found no effect. Moore (1964) and Lubar (1964) reported the same for cats, and the former reported a <u>retention</u> deficit in five cats as well. With the exception of Moore (1964) and the present investigation, there have been no published reports of retention studies of shuttlebox performance, and so further research will be necessary to clarify these findings.

PAR, mouth-shock. On the basis of errors alone, the hypothesis concerning this task was confirmed, for none of the rats showed a significant change following either lesion. Group M even improved after the first lesion.

PAR, hindleg-shock. The hypothesis of a deficit in this task following the midcingulum lesion was not confirmed; but the hypothesis (2bi) that the genual lesion would combine with the midcingulum lesion to produce a deficit in the retention of this task was confirmed. Three rats made significantly more errors postoperatively in this task: # 15 after the midcingulum lesion, and ## 17 and 18 after the genual lesion. The combination of the two lesions produced a significant deficit in group G.

When the animal experiences shock to the hindlegs, this is experienced via the posterior cingulate gyrus, appraised as painful, and remembered. Afterwards, movement toward the water would normally be inhibited, since it is now appraised as inappropriate, because of the affective memory of the pain. With the cingulum interrupted just caudal to the anterior cingulate gyrus, the animal may still be able to appraise its movements as inappropriate, but the impulse to revive earlier appraisals of movements in such situations (affective memory, mediated by the cingulum), although it may be initiated via intact anterior cingulate cortex, cannot be transmitted via the cingulum to the hippocampus-fornix system; hence, the thirsty animal no longer experiences a reluctance to move toward the water it wants. As a result, it approaches and drinks, and a PAR deficit is revealed.

But when the shock has been to the mouth, it is primarily the head and mouth movement that is appraised as inappropriate (via the anterior insula). Since the anterior insula is intact, but the cingulum is lesioned (both at area 23 and at the genu of the corpus callosum in area 24), the rat may approach the cup, but then experiences a reluctance to dip its head into the water because its affective memory for head movement is intact. While the anterior insula may be intact, rats which are shocked in the hindlegs should not necessarily connect that movement of the head with the shock they feel in the hindlegs when they drink. This difference between the two tasks (one with hindleg-shock producing a reluctance with respect to bodily movement and the other with mouth-shock producing a reluctance to dip the head toward the water) accounts for the different error scores of the two tasks. This explanation receives support from Kaada et al. (1962) who found that rats with insular lesions made sixteen-times more errors than normal controls in a PAR task with mouth-shock; on the other hand, the mean number of "approach-withdrawal responses" (our "complete approach") for normals was 13.4, and for the insular lesioned rats 10.4.

Retention vs. learning. There is no precedent in the literature for a retention study of these two PAR tasks; however, a recent study in the Behavior Laboratory (Arnold & Mead, 1969) found that rats with cingulotomies at area 23 performed significantly worse than normal controls in the acquisition of both of the PAR tasks of the present study. With cingulum lesions at area 23, learning should be impaired more than retention, no matter what the task. When a task is being learned, the movement to be acquired must be appraised as successful or unsuccessful so that successful movements can be retained and repeated in response to the appropriate visual, auditory, or other cue. In contrast, once the task is learned, the positive cue is immediately appraised as good for action, and produces an action impulse which nees no further appraisal unless it is to be inhibited.

"Complete approach". This phenomenon is a noteworthy observation of the present investigation, and throws light on the celebrated "approach-avoidance conflict." In both PAR tasks, following the first lesion and the combination of the two lesions (measured by a comparison of R_1 and R_3), bilaterally cingulotomized rats made significantly more complete approaches. When shock was delivered to the mouth, individual analysis revealed that five rats of the M group and none of the MI group made significantly more complete approaches; and when shock was to the hindlegs, four of the M group and none of the MI group made significantly more complete approaches.

McCleary (1961; see also Lubar & Perachio, 1965) said that "the passive avoidance test seems to involve a more obvious approach-avoidance conflict situation than does the active avoidance test (p. 611)," and it is likely that the hyperactivity his cats showed between PAR trials is similar to what we observed in rats. Boctano & Isaacson (1967), Kaada et al. (1962), and Naess & Rasmussen (1958) have reported such "approach-withdrawal" behavior. Kaada et al. (1962) describe "intention movements" which are very similar to our own observations:

> The animal approached the dish slowly and cautiously and then withdrew quickly. Occasionally it remained motionless for several seconds, leaning over the dish and then suddenly withdrawing. Some rats would stand motionlessly on the same spot and only make a number of intention movements or, on some occasions, they might move just the forelegs. Only those responses consisting of forward movement of the entire body and subsequent withdrawal were actually recorded as approach-withdrawal responses (p. 662).

We did not score such "foreward movements," which we classified as "partial approaches;" only when the animal was clearly only a few millimeters away from shock and in good physical contact with one of the electrical poles was it judged to have made a "complete approach." Kaada et al. (1962) state that "clearly, approach-withdrawal responses are not as sensitive a measure as is the number of shock responses (p. 668)," and we agree in part; but these investigators used a low level of shock (.183 ma.). If they had used a level of shock as high as ours (2.5 ma.) they might have found more dramatic results in the form of fewer errors and more "approach-withdrawal responses." It must also be remembered that "complete approaches" and errors are mutually exclusive: one or the other of these kinds of responses may be observed, but not both in one animal at the same time. Since this is the case (see Table 1 in the Kaada et al., 1962 study), and since, as Kaada et al. (1962) admit, there are several other forms of behavior which are observed in a PAR situation which are neither errors nor "approach-withdrawal responses," it seems reasonable to say that both errors and "approach-withdrawal responses" may be used as measures of PAR deficit in rats.

Conclusions

At the beginning of this dissertation, it was stated that the purpose was to test a particular part of Arnold's (1960a) theory of brain functioning, namely, her suggestion that the cingulum, as the link between the limbic cortex of the anterior cingulate gyrus and the hippocampal-fornix system (relays from which return to the anterior cingulate gyrus), mediates the psychological function of affective memory of movements and movement impulses. The theory was that (a) bilateral severance of the cingulum caudal to the anterior cingulate gyrus (area 23 in the rat) would, by blocking impulses from anterior cingulate cortex to the hippocampus, impair affective memory of movements;

and (b) bilateral interruption of the cingulum at the genu of the corpus callosum, by blocking impulses from subcallosal and precallosal limbic cortex, would also impair affective memory of movements.

The behavioral measures of the effects of these lesions were chosen to (a) directly test the postulated circuit for the affective memory of movements (both PAR tasks), and (b) to control for the possible effects of damage to this circuit on the retention of visual and olfactory discrimination, and two-way AAR.

Midcingulum lesion. From our findings we are able to conclude that bilateral interruptions of the cingulum at area 23 in rats produces a significant change in the motor performance of rats in several tasks, which change is most reasonably interpreted as indicating an impairment in the affective memory of movements. First, group M made significantly more bar-presses after the midcingulum lesion; second, this group made significantly more "complete approaches" in both PAR tasks after the same lesion. On the other hand, cingulotomy at area 23 in rats does not have a detrimental effect on the retention of visual or olfactory discrimination, of two-way AAR, or of PAR, either with mouth-shock or hindleg-shock; no deficits were observed in group M in any of the five tasks.

After the midcingulum lesion group M made significantly fewer errors in PAR, mouth-shock, and did not change significantly in PAR, hindleg-shock; this fact leads to the conclusion that the dominant process involved in learning and retaining the PAR, mouth-shock, habit is the rat's capacity to appraise somesthetic impressions and movements of the head via the insula. The fact that PAR, hindleg-shock, was not significantly affected by midcingulum lesions may be due to the possibility mentioned above (p. 14), that many fibers leave the cingulum anterior to the lesion site to penetrate the corpus callosum and join the fornix, so that the lesion would have comparatively little effect on this PAR task.

Combination of midcingulum and genual lesions. Bilateral interruption of the cingulum at the genu (area 24), following the midcingulum lesion, resulted in a significant deficit in the retention of PAR, hindleg-shock, while there was no impairment in any of the other tasks. The deficit in PAR, hindleg-shock, cannot be due to an impairment in the appraisal of somesthetic impressions (pain), because AAR also depends on this and was unimpaired. The deficit also cannot be the result of a general motor disfunction, because the lesioned animals did not appear to have any difficulty in bar-pressing and in the movements required in the other tasks (or, for that matter, in moving around in their home cages). Finally, the deficit cannot be the result of an impairment in motor memory (as might be suspected from the incidental damage to the hippocampal rudiment), for the simple reason that such a deficit would not be revealed in any of the tasks used in this study, since visual cues were always available. According to Arnold's theory, impairment in motor memory is revealed only in tasks which have no sensory cues, i.e., tasks in which the animal must recall what it had done or had intended to do in the past (e.g., right/left alternation, delayed response).

From the fact that a combination of midcingulum and genual lesions produced an impairment in PAR, hindleg-shock, while the midcingulum lesions alone did not, it can be inferred that a considerable number of cingulum fibers must penetrate the corpus callosum and join the fornix anterior to area 23 in the rat.

In addition, this combination of lesions produced a significant decrement in the number of positive reinforcements attained by group G in the visual discrimination task. This deficit cannot be the result of decreased thirst, because the group with midcingulum lesions, under identical conditions did not exhibit such a change. In fact, fewer reinforcements should result in greater thirst as the trials continue. Since there is no indication of any extrinsic influence, it seems reasonable to conclude that the number of successful bar-presses declined for the same reason that the total number of bar-presses increased in group M: the animals were no longer able to gauge the appropriateness of their movements in bar-pressing because the cingulum lesions had impaired their affective memory for foreleg-movement (see p. 66).

Suggestions for further research. While the findings of this study confirm Arnold's theory with respect to the function mediated by the anterior cingulum, and, by exclusion, indirectly support her theory of the function served by the insula, nevertheless, they have also brought to light several problems which demand further investigation. First, since the two PAR tasks were performed in two different apparatuses, it is not certain whether the obtained differences in performance are not due, in part, to the differences in the two PAR situations. To differentiate between the retention of PAR tasks with mouth-shock and hindleg-shock, with a higher degree of probability, two groups of rats should be trained in an apparatus similiar to the one described here for PAR, mouth-shock. One group would be shocked in the mouth while drinking, the other shocked in the hindlegs while drinking. The same experiment could, of course, be done by using the apparatus described here for PAR, hindleg-shock. Second, further research is necessary to discover the effects on normal rats of differences in CS, CS-US interval, trial duration, etc., in the shuttlebox. If the parameters of this popular apparatus could be standardized, experiments by different researchers would be truly comparable with respect to instrumentation. Third, it would be desirable to systematically study the effects of small interruptions of the cingulum at six equally distributed sites from the genu to the splenium of the corpus callosum. This should reveal a differential effect of cingulotomy on affective memory and demarcate more precisely the cingulate area which mediates the appraisal of movements from that which mediates the appraisal of somesthetic impressions. Fourth, since the hippocampal rudiment was interrupted in the majority of the rats of this study, it is not clear whether the role of this pathway is independent of the role of the cingulum with respect to affective memory. The following experiment would contribute to the solution of this difficulty: after training in PAR, AAR, and single alternation, 100 rats would be randomly assigned to four equal groups: group A would receive cingulotomy at area 23 (with the hippocampal rudiment spared), group B would receive interruptions of both the cingulum and the hippocampal rudiment at the same site, group C would receive a transection of the hippocampal rudiment at the same site, and group D would be operated controls. Such an experiment would be expected to clarify the role of the cingulum and the hippocampal rudiment both with regard to the mediation of simple motor memory and affective memory of movements and movement impulses, and would be able to build on the findings of the present study.

ABSTRACT

Arnold's theory that the anterior cingulum mediates the affective memory of body movements was tested with a before-and-after design. Sixteen rats were trained in visual and olfactory discrimination, two-way AAR, and two passive avoidance (PAR) tasks, one with mouth-shock, the other with hindleg-shock. Then Ss were tested for preoperative retention, received bilateral lesions of the cingulum at the midcingulate area, were tested for postoperative retention, received a second cingulotomy at the genu of the corpus callosum, and were tested for retention. The first lesion significantly increased "approach-withdrawal responses" in both PAR tasks. The combined effect of both lesions was a significant deficit in PAR, hindleg-shock. The results were interpreted as confirming Arnold's theory.

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APPROVAL SHEET

The dissertation submitted by Bert Mead, S.J. has been read and approved by three members of the Department of Psychology.

The final copies have been examined by the director of the dissertation and the signature which appears below verifies the fact that any necessary changes have been incorporated, and that the dissertation is now given final approval with reference to content and form.

The dissertation is therefore accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 13, 1969
Date

Magda B. Arnold
Signature of Advisor