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The Effect of Bilateral Lesions of the Cingulum on the Retention of Five Sensory Modalities in the Albino Rat

by

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CHAPTER I

INTRODUCTION

In 1937 Papez proposed that the hypothalamus, the anterior thalamic nuclei, the cingulate gyrus, the hippocampus and their interconnections represent an anatomical circuit for emotions. This hypothesis has found support in a number of studies in which emotional changes were reported in experimental animals with cingulate ablations. This theory of emotional functioning has culminated in the comprehensive theory of brain functioning developed by Magda B. Arnold.

The purpose of this experiment is to study the function of the cingulum, an integral part of this circuit. It will test Arnold's hypothesis that the cingulum mediates affective memory in the hippocampal-cingulate circuit. In particular, it is proposed to test the hypothesis that an interruption of the cingulum will result in modality-specific deficits in affective memory which will leave the subjects unable to perform a previously learned task involving the affected modality.

The cingulum is a fiber bundle which includes projections from the anterior thalamic nuceus as well as cingulate cortical areas. Kaada (1960) reports that the thalamocingulate projections are derived from all three portions of this nucleus: the agranular anterior cingulate area (Brodmann's area 24) receiving fibers from the anteromedial nucleus; the granular posterior cingulate area (Brodmann's area 23) receiving fibers from the anteroventral nucleus; and the retrosplenial regions (Brodmann's areas 29 and 30) receiving fibers from the anterodorsal nucleus. In all these cortical areas (as well as the granular prefrontal cortex) fibers of the cingulum bundle originate and run through the white matter in the retrosplenial region. The projection from the anterior thalamic nucleus runs forward in a wide arc through the internal capsule, past the anterior horn of the lateral ventricle and reaches the cingulate cortex from a lateral direction at the level of the genu of the corpus callosum. The cingulum is formed from cortical afferents and runs caudally through the cingulate and retrosplenial gyrus to the hippocampal gyrus.

The cingulum fibers thus complete a circuit between the cingulate cortex and the hippocampus. This circuit can be traced from the hippocampus through the fornix via the mammillary bodies through the anterior thalamic nucleus to the cingulate gyrus and is finally completed by the cingulum to the hippocampal gyrus and possibly to the hippocampus (Kaada, 1960). All of these structures are part of an interrelated system which Broca termed the "limbic lobe".

Papez (1937) first suggested that these structures are part of an emotional circuit and mediate what he called the "stream of feeling". In a later article (1939) he ascribed to this circuit the stream of excitations that "underlies general consciousness and the emotive reactions". Unlike earlier theorists he postulated a definite cortical center of emotion, the cingulate cortex and indicated many possible circuits connecting with this area. MacLean (1949), following up the implications of Papez' theory, suggested that the cingulate gyrus is part of the "visceral brain" supposedly concerned with visceral and emotional functions. MacLean proposed that the whole hippocampal area is a correlation center for all sensation and that its connection with the hypothalamus provides these impressions with emotional coloring as well as an autonomic effector organ.

Since MacLean's article a great many studies have attempted to throw light on the function of the cingulate gyrus, an integral part of the emotional circuit discussed by both Papez and MacLean. In 1954, MacLean reported that electrical and chemical stimulation of the posterior cingulate gyrus aroused increased pleasure reaction to petting in cats. Sexual excitation was also shown in some of the experimental animals. Stamm (1955) reported that rats with lesions in the medial cortex did not let their young suckle, did not protect them from an airblast or cover them with paper strips to protect them from heat, as did normal rats. Instead, they ran around aimlessly when exposed to airblasts or heat, picked up their litter, but soon dropped the young in any part of the cage. Ward (1948) has reported the behavior of monkeys which had the anterior cingulate gyrus removed. These monkeys lost their operative shyness with man and were much more inquisitive. They lacked the normal grooming behavior and did not exhibit the acts of affection towards their companions found in intact monkeys. Instead they treated their companions like inanimate objects and would walk on them, bump into them and even sit on them. They would openly eat food from another monkey's hand without expectation of being attacked and be surprised when the attack came. Despite all this behavior these monkeys never showed actual hostility towards their companions.

Magda B. Arnold (1960) has evaluated these and many other experimental reports and has evolved an inclusive theory of brain functioning. She has concluded that the limbic cortex mediates appraisal, experienced as liking or disliking. Specifically, she has hypothesized that the subcallosal gyrus mediates the appraisal of odors, the anterior cingulate gyrus the appraisal of actions and action impluses, and the posterior cingulate gyrus mediates the appraisal of touch. She has proposed that the cingulum serves the revival of affective memory in these various sensory and action modalities when impulses relayed via the fornix, mamillary body, and anterior thalamus and cingulum reach the appropriate limbic area. Thus the appraisal of odors as pleasant or unpleasant would be revived when these impulses reach the subcallosal gyrus, the memory of appropriate or inappropriate actions when they reach the anterior cingulate gyrus, and the memory of pleasant or painful touch when they reach the posterior cingulate gyrus. This study serves as a test of the role of the cingulum in this theoretical conception of brain functioning.

In brief, small lesions will be placed bilaterally in the cingulum at the junction of the motor and somatosensory cortex. According to Arnold's theory, this should interfere with affective memory (i.e. the memory of pain or pleasure, punishment or reward, and the memory of successful and unsuccessful actions). As a result, there should be a retention deficit in various discriminations. However, this deficit is not expected to be very pronounced because discrimination learning depends not only on the memory of reward or punishment but also on remembering which cue is positive and which negative, that is, on "modality-specific" memory. According to Arnold, such modality-specific memory is mediated by relays via the hippocampal rudiment and hippocampus to fornix, sensory thalamic nuclei and cortical association area and should not be affected by the lesion.

Olfactory, tactual, visual and auditory discrimination will be used to investigate the effect of such a lesion on retention, in every sensory modality. In addition, the single alternation T-maze will serve to study the effect of this lesion on a performance depending on motor memory.

CHAPTER II
METHOD

Subjects

Sixteen naive albino rats (approximately one year old at the beginning of training) were gentled and trained on five different discriminations. They were purchased from the Holtzman Company of Madison, Wisconsin; their sated weights ranged from 400 to 500 grams. Throughout the experiment the rats' temperaments appeared to remain constant.

Apparatus and Tasks

Olfactory Discrimination: The olfactory apparatus is basically a narrow box with high walls. In front of this box is a glass face and a mounting ledge. Between the glass face and mounting ledge is a trough with a sliding wooden bar. This bar has stainless steel cups placed in it at intervals of 3 inches so that only one cup is within the walls of the apparatus at one time. These cups are partially filled with paraffin so that the animal gets only a small amount of water. The animal must discriminate between the odors of lemon as a positive stimulus and vanilla as a negative stimulus. While the lemon cups contained clear water the vanilla cups contain a quinine soluation which is extremely bitter.

Visual Discrimination: Small animal test chambers (Skinner boxes) manufactured by the Foringer Company, Model #1102-ml, were used in conjunction with the necessary programming accessories.

The chambers are constructed with two white lights mounted above the bar on one wall. The positive stimulus consists of the flashing of these lights approximately 3 times per second. A bar press during this sequence is rewarded with one dipper of water. A bar press made while the lights are steady (not flashing) results in a mild electrical shock to the feet. The onset and cycling of all stimuli is done electronically. Timers, in combination with a sequence alternator panel, present lights-flashing and lights-steady phases in a random cycle. The duration of each phase is 22 seconds. Daily sessions were 15 minutes per day. Responses are electrically recorded as correct or incorrect and as shocks or reinforcements.

<u>Auditory Discrimination</u>: Small animal test chambers (Skinner boxes) manufactured by the Foringer Company, Model #1102-ml, were used in conjunction with the necessary programming accessories. The positive discriminative stimulus consists of a clicking sound produced by a sound generator and channeled into the testing room via a Quam 8½ inch speaker. The speaker is outside the test apparatus to avoid vibration. The onset and cycling of all stimuli is done electronically. Timers in combination with a sequence alternator panel, present sound-on, sound-off phases in a random cycle. The duration of each cycle is 22 seconds. Daily sessions were 15 minutes per day. The reward for a correct bar press is one dipper of water, while an incorrect response brings an electrical shock to the feet. Responses are electrically recorded

as correct or incorrect, and as shocks or reinforcements.

Single Alternation: The single alternation is basically a T-maze with one choice point. The animal is required to perform a delayed alternation task, with water reward for correct choice, no reward for incorrect choice. The apparatus is equipped with return alleys so that the animals are handled as little as possible. The maze is completely covered up to the choice point and is run in darkness except for a small red light for observation. As in all other discriminations (except auditory and olfactory) a speaker provides white noise. The maze is also equipped with an illuminated start box and hinged doors at the choice point.

Tactual and Pain Discrimination: This apparatus is the same as that used for the visual and auditory discriminations. However neither visual nor auditory cues will be available (i.e. no lights or clicking sounds). Instead the animal must probe his way through the session; he must keep testing the bar to see whether he will get water and no shock or shock and no water. The schedule for reinforcement consisted of 15 second cycles, one-half positive and one-half negative, in a random sequence. The rat learns to press rapidly whenever he feels no shock and to slow down when he does feel a shock to his hind feet. That this indeed represents a discrimination was tested by comparing the performance of the same 16 rats on two separate five-day retention periods, which differed only in that shock was available in one and not in the other. As expected, the accuracy of probing with no shock is significantly lower than with shock, at the .001 level. With shock most rats probe with an accuracy of 60-70 per cent correct. Without shock they probe with an accuracy of 53 per cent or lower.

Procedure

Intially the rats were deprived of water for 24 hours. They were then trained on the five discriminations to an average of 90 per cent correct responses over three successive days (with the exception of the tactual discrimination where the criterion had been empirically determined at 60 per cent correct). Once they had mastered all discriminations, they were sated and given a 10 day rest period. They were deprived of water on the last two days of this rest period. They then underwent the first 5 day retention period, being tested daily on all five discriminations. The sequence of daily tests was always: single alternation, tactual, olfactory, auditory, and visual. The time of day for running each test remained constant. During a retention period, the only water the rats received was the water they obtained in the test situations, which was more than sufficient to maintain them. Throughout the study the animals were provided with <u>ad lib</u> access to food. Since the animals were intact during the first retention period (R_1), their scores during R_1 served as a control against which their scores in R_2 were compared. In the 10 day rest period between R_1 and R_2 the animals received cingulum lesions adjacent to the somatosensory cortex.

Operations

The animals were anesthetized by placing them in a four liter chamber, into which a gaseous mixture of ether and air was pumped. After two minutes of anesthetic the animals were given a .20 cc. intraperitoneal injection of Nembutal, followed by a few more minutes of ether, if it were required. Clean surgical techniques were used. The animal's head was shaved and washed with alcohol. The scalp was opened at the midline and the periosteum was scraped aside. Trephine holes were then bored with a dental drill fitted with #2 round burrs. Electrodes of .046 inch in diameter and coated with Formvar except for a 1mm. tip exposure were used to make the lesion. The lesions were made with a Grass Radiofrequency Lesion Maker, Model Lm-3, and monitored with a Knight Milliammeter. Monoploar electrodes (with the animal serving as a ground) were placed bilaterally 2mm. behind the bregma, 1mm. laterally, and 3mm. beneath the surface of the skull. These coordinates had been determined empirically as transecting the cingulum at the junction of the motor and somatosensory cortex. A current of 35 milliamperes for 15 seconds was used in lesioning the animals. Then a spray antiseptic was applied and suture clips were used to close the wound. Throughout the operation the rat was fixed in a Krieg-Johnson stereotaxic apparatus, which had been modified to preclude the use of earplugs. The use of earplugs provided with this apparatus had been found to cause auditory deficits and uncoordinated movements in otherwise intact animals.

Histology

The animals were sacrificed and perfused with isotonic saline and 10 per cent formalin. Their brains were extruded, trimmed, left in 10 per cent formalin for 2 - 4 weeks, mounted in parraffin, and cut in 5 microns thickness. Serial sections of the lesion sites were stained with hematoxylin and eosin. Slides were read by the author and Victor Dufour.

CHAPTER III

RESULTS

Table 1 is a summary of lesion damage and deficits. In all but one animal (4) the cingulum was transected bilaterally. In all but two animals, the indusium griseum was also transected bilaterally. The corpus callosum which lies ventral to these structures was transected in all the animals. The hippocampus received minimal damage in five of the animals and extensive damage in three of them. The superior fornix received extensive damage in two animals. Various areas of the cortex were damaged in different animals with only the posterior cingulate cortex receiving extensive damage in all the animals. The lesions averaged 4.5 millimeters along the anterior-posterior axis and 4.0 millimeters along the medial-lateral axis.

Figure 1 shows cross sections of brains of all the experimental animals with the lesions at their maximal extent. The micron (μ) designations refer to the anterior-posterior position of each slide and are based on the Konig and Klippel Atlas (1963). The micron (μ) range is from 480μ, posterior pole (not including cerebellum), to 13760μ, anterior pole. Figure 2 is a diagram of the most important structures involved in these lesions.

Table 2 presents the R_1 and R_2 of each subject on each discrimination. Also presented are the mean difference, standard deviation and the final <u>t</u> for each of the R_1 — R_2 comparisons.

Significant differences are indicated at the .025, .01 and .005 levels.

There were two animals which exhibited deficits in the single alternation. There were an additional three animals which refused (i.e. they would not or could not run) in the alternation task. Three of the animals displayed deficits in the tactual discrimination task and one showed an auditory discrimination deficit.

Table 1

Lesion Damage and Deficits

		Animal #										
		2	3	4	5	6	7	9	10	11	12	14
Structures Damaged	cingulum	X	X	U	X	X	X	X	X	X	X	X
	indusium griseum	X	X	U	X	X	X	X	X		X	X
	corpus callosum	X	X	U	X	X	X	X	X	X	X	X
	hippocampus	1	3	1	1	1			1		3	3
	superior fornix										3	3
Cortical Areas Damaged	6	1	2		2	2	2	1			2	2
	4	2	2	2	2	2	2	2	1	1	2	2
	3	2	2		2	2					1	1
	7	1	1	1	1	1		1	1	1	1	1
	18								1		1	1
	24	1	1		1						1	1
	23	3	3	3	3	3	3	3	2	3	3	3
	29	1	1	1	1	1		1	2	1	2	2
Functional Deficits	alternation										.005	.005
	refuser*	X					X		X			
	tactual	.025	.025			.01	.025					
	auditory				.005							

X structure transected bilaterally
U structure transected unilaterally
1 area damaged minimally
2 area damaged moderately
3 area damaged severely
* These animals would not or could not perform the alternation task.

Table 2
Task Data

Animal	Discrimination	R_1	R_2	Mean Dif.	Std. Dev.	t
2	Olfactory	88.00	90.00	-2.00	4.47	-1.000
	Visual	91.60	80.00	11.60	13.90	1.866
	Auditory	87.75	84.00	3.75	19.75	0.380
	Alternation	9.40	R			
	Tactual	66.25	52.75	13.50	8.54	3.160*
3	Olfactory	90.00	98.00	-8.00	13.03	-1.372
	Visual	85.25	83.00	2.25	13.32	0.338
	Auditory	94.60	82.20	12.40	11.52	2.406
	Alternation	7.80	6.00	1.80	2.59	1.555
	Tactual	62.80	53.00	9.80	8.11	2.704*
4	Olfactory	86.00	98.00	-12.00	4.47	-6.000
	Visual	83.20	89.80	-6.60	8.08	-1.826
	Auditory	88.00	85.75	2.25	6.40	0.704
	Alternation	8.40	6.60	1.80	1.64	2.449
	Tactual	63.00	57.80	5.20	10.80	1.076
5	Olfactory	90.00	90.00	-4.00	15.17	-0.590
	Visual	92.60	84.00	8.60	10.48	1.835
	Auditory	92.80	75.40	17.40	6.07	6.414#
	Alternation	7.40	7.40	0.00	2.24	0.000
	Tactual	66.75	59.50	7.25	11.44	1.267
6	Olfactory	76.00	92.00	-16.00	21.91	-1.633
	Visual	91.80	84.80	7.00	14.19	1.103
	Auditory	91.80	73.20	18.60	17.30	2.404
	Alternation	8.40	8.20	0.20	1.30	0.343
	Tactual	62.20	40.20	22.00	11.34	4.340**
7	Olfactory	100.00	100.00	-6.00	5.48	-2.450
	Visual	95.50	88.50	7.00	6.32	2.214
	Auditory	97.20	85.80	11.40	8.17	3.119
	Alternation	8.80	R			
	Tactual	71.33	54.33	17.00	8.66	3.400*

Table 2 (Continued)

Animal	Discrimination	R_1	R_2	Mean Dif.	Std. Dev.	t
9	Olfactory	96.00	96.00	0.00	7.07	0.000
	Visual	89.40	90.40	-1.00	9.49	-0.236
	Auditory	91.75	91.25	.050	7.59	0.132
	Alternation	8.40	6.20	2.20	1.48	3.317
	Tactual	61.00	47.40	13.60	15.65	1.944
10	Olfactory	84.00	94.00	-10.00	15.81	-1.414
	Visual	88.20	88.60	-0.40	2.88	-0.310
	Auditory	84.40	85.80	-1.40	12.30	-0.255
	Alternation	8.60	R			
	Tactual	55.40	54.00	1.40	5.55	0.564
11	Olfactory	98.00	100.00	-2.00	4.47	-1.000
	Visual	93.50	96.50	-3.00	6.93	-0.866
	Auditory	97.80	97.80	0.00	1.58	0.000
	Alternation	7.80	7.80	0.00	0.89	0.000
	Tactual	67.00	70.50	-3.50	0.71	-7.000
12	Olfactory	90.00	100.00	-10.00	12.25	-1.826
	Visual	97.60	91.40	6.20	6.06	2.288
	Auditory	96.80	95.80	1.00	2.92	0.767
	Alternation	7.80	4.80	3.00	0.71	9.487#
	Tactual	67.80	64.80	3.00	11.56	0.410
14	Olfactory	96.00	100.00	-4.00	5.47	-1.633
	Visual	92.50	94.25	-1.75	3.30	-1.059
	Auditory	93.00	94.40	-1.40	4.22	-0.742
	Alternation	7.25	2.75	4.50	1.00	9.000#
	Tactual	62.40	57.80	4.60	5.18	1.987

* Beyond the .025 level
**Beyond the .01 level
\# Beyond the .005 level
R These animals would or could not perform the alternation task in the R_2.

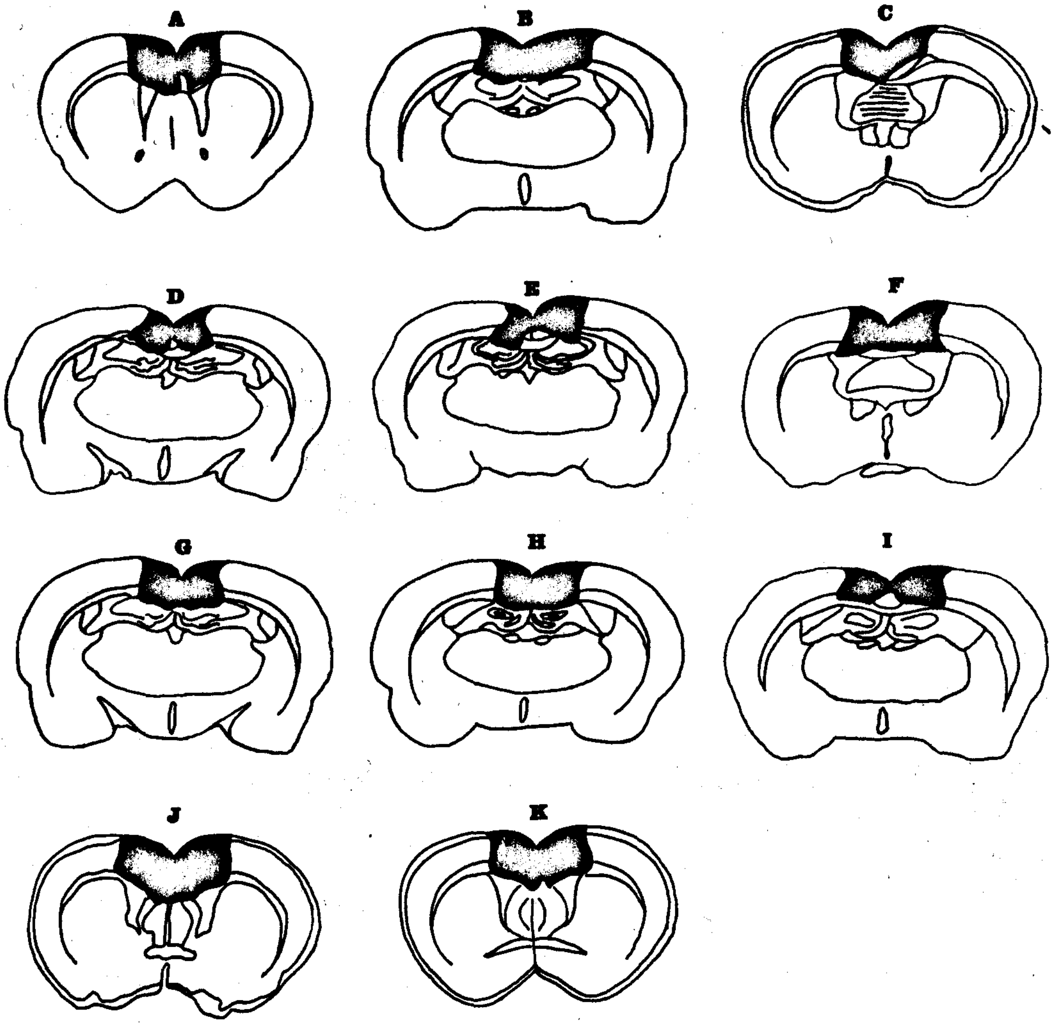

Fig. 1. Cross sections of brains showing lesions at their maximal extent.

(A) Animal 2 at 7400μ
(B) Animal 3 at 4700μ
(C) Animal 4 at 6500μ
(D) Animal 5 at 4350μ
(E) Animal 6 at 4400μ
(F) Animal 7 at 6600μ
(G) Animal 9 at 4400μ
(H) Animal 10 at 5200μ
(I) Animal 11 at 5000μ
(J) Animal 12 at 6900μ
(K) Animal 14 at 6800μ

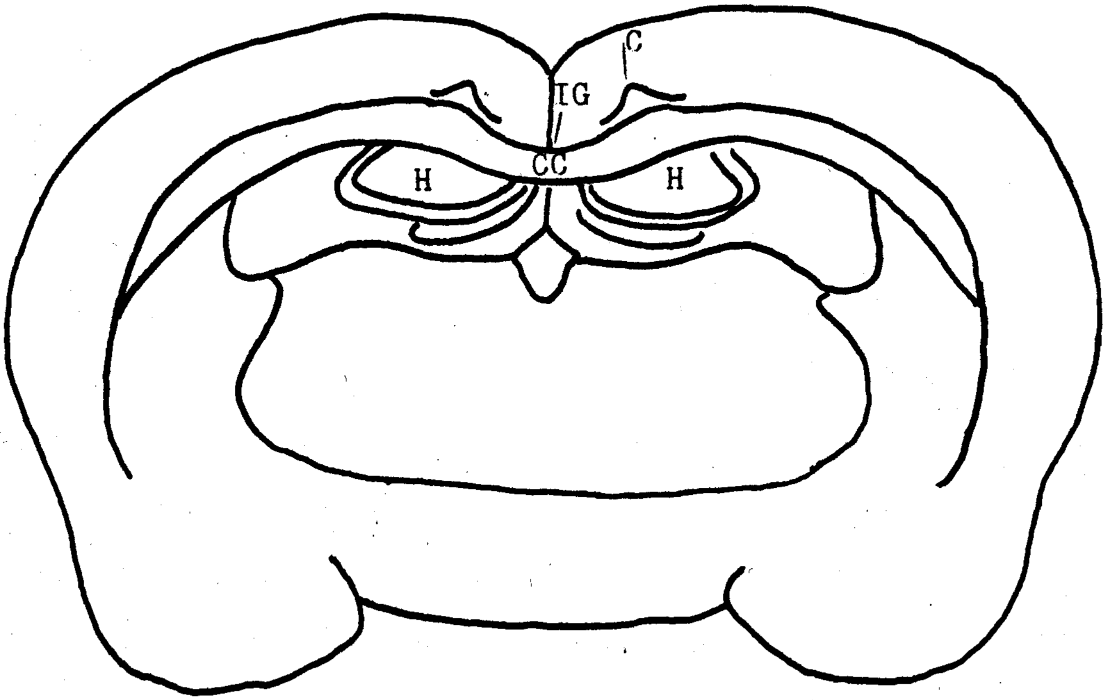

Fig. 2. Diagram of the most significant structures damaged.

C - cingulum
CC - corpus callosum
IG - indusium griseum
H - hippocampus

CHAPTER IV

DISCUSSION

It is regrettable that the lesions were so large. They not only transected the cingulum as intended; in many cases they also damaged the hippocampal rudiment, cingulate and retrosplenial gyri, transected the corpus callosum and encroached slightly on the hippocampus. This makes it difficult to attribute the observed deficits to the destruction of specific structures and so relate them to Arnold's conception of modality-specific or affective memory.

However, according to Table 2, all animals except #11 had some decrement in performance when the postoperative R_2 is compared to the preoperative R_1 though the difference was not always significant. Animal #11 remained stationary or improved in all tasks. This animal had the smallest lesion which was confined to the cingulate gyrus and cingulum, with the hippocampal rudiment and hippocampus intact. Indeed, the cingulum damage was confined to the medial part on both sides, which might account for the absence of any deficit.

Of the various discriminations in the test battery, the <u>tactual</u> discrimination should be affected most by the lesion because the only cue provided was shock to the hind legs which, according to Arnold, is mediated by the posterior cingulate and retrosplenial gyri, and is recalled when impulses are relayed via cingulum, fornix and anterior thalamic nucleus back to these areas. Consequently, the discrimination depends almost exclusively on affective memory. The performance affected least should be the olfactory discrimination because the pleasantness of drinking water and the unpleasantness of tasting quinine is, according to this theory, experienced via the posterior insula; from there, the affective memory circuit is thought to go via claustrum, hippocampus and fornix to return eventually to the posterior insula. The cingulum lesion in this experiment did not interfere with this circuit.

In line with expectation, the data show that the olfactory discrimination is the only one that showed improvement in every animal from R_1 to R_2 except for animal #9 which remained stationary. On the other hand, every animal except #11 showed a deficit in the tactual discrimination, though the difference between R_1 and R_2 reaches significance only in animals #2, 3, 5 and 7, which is what would be expected on the basis of the theory.

Visual and auditory discrimination tasks offer visual and auditory cues in addition to shock to the hind legs after an erroneous bar press. Thus the affective memory of pain is supplemented by visual or auditory memory. According to Arnold, visual and auditory memory are mediated via the hippocampus-fornix system. This means that visual and auditory discrimination should be adversely affected by damage to the hippocampus, but also by lesions of the cingulum (which mediates affective memory). But the hippocampal lesions in this experiment were small and superficial when compared to the lesions that previously have produced deficits in auditory and visual discrimination: Driessen (1964) reported such deficits after complete bilateral hippocampal transections; Niki (1962) found a deficit in visual discrimination after deep bilateral lesions in the dorsal hippocampus; Kimble (1963), after lesions that destroyed the greater part of both hippocampi. Consequently, we cannot expect much visual or auditory memory deficits and the expected affective memory deficit could be reduced because visual and auditory cues can still be used.

In the <u>visual</u> discrimination according to Table 2 animals #4, 9, 10, 11 and 14 showed some postoperative improvement in R_2. The other six animals showed a slight deficit which, however, did not reach significance in any animal. In auditory discrimination, the deficit is slightly greater: Two animals (#10, 14) were minimally improved from R_1 to R_2, #11 remained stationary, and eight animals showed deficits which in one case (#5) were statistically significant. For the reasons stated above, this deficit can be considered the result of the damage to the cingulum rather than to the hippocampus and thus can be explained as an impairment of affective memory.

<u>Deficits and refusals in single alternation</u>. Single alternation seems to require motor memory and imagination. The animal must recall that the last turn was "this way" and this turn is "the other way". A lesion of the cingulate cortex at the junction of

motor and somatosensory area would interfere with the appraisal of movement as suitable or unsuitable; and a lesion of the cingulum would interfere with recalling that this movement had been "good" (or successful) and that one "bad" (or unsuccessful), so that the animal would have no impetus to move in either direction. In addition, the motor memory of having gone left or right the last time would be impaired by a lesion of the hippocampal rudiment.

Of the eleven experimental animals, only two (#5 and 11) did as well in R_2 as they had done preoperatively in R_1. Six animals made poorer scores in R_2 (#3,4,6,9,12,14) but only in the latter two animals was the difference significant. The remaining three animals (#2,7, 10) refused to run altogether (see Table 2). Behavioral observation suggests that animals #12 and 14 had forgotten which alley to take. They set out quickly and willingly but made many errors. But the three "refusers" did not seem to have any impetus to move. They were quite unlike the occasional animal met in training which seems to have the greatest difficulty learning the discrimination. These problem learners usually seem frightened and take refuge in the covered portion of the apparatus where they hide. The "refusers", on the other hand, did not appear excited or frightened and would spend most of their time in the starting box and the uncovered portion of the alternation apparatus. They seemed healthy enough but would not run to the choice point. Eventually, they tended to stop all activity and remain in one spot.

The two animals which showed a significant increase in errors in R_2 had (in addition to damage in the hippocampal rudiment, cingulate gyrus and cingulum) a large lesion in the superior fornix. According to recent reports (Raisman et al, 1965) the superior fornix carries afferent as well as efferent fibers and so may participate in the circuit from anterior cingulate to hippocampal rudiment and hippocampus (Arnold's "action circuit" which activates motor memories). The "refusers", on the other hand, might have lacked any impetus to run because of the injury to cingulate gyrus and cingulum. Perhaps increased thirst could supply the missing action impulse in these animals; unfortunately, this possibility was not investigated in this experiment.

In summary, the deficits found in this study do allow an interpretation on the basis of Arnold's theory. The only other hypothesis available, that of McCleary (1961) who postulated that the cingulate gyrus is a "facilitatory motor area", is so broad that it is not applicable in the present context. Apart from the fact that McCleary's lesions (which produced an active avoidance deficit) involved almost one whole of the cingulate gyrus from genu to splenium on both sides while our lesions are comparatively small, the deficits reported in the present study can hardly be the result of a "motor facilitation".

The additional lesions of the hippocampal rudiment and superior fornix have made the interpretation more difficult but not impossible. An earlier study by Gavin (1963) also reports a deficit in single alternation after hippocampal rudiment lesion; and Dufour (1967) found that 50% of the animals with lesions in the cingulate gyrus and hippocampal rudiment refused to perform either in the olfactory discrimination or the single alternation apparatus, though he ascribes this phenomenon to accidental factors.

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APPROVAL SHEET

The thesis submitted by John E. Conneely has been read and approved by the director of the thesis. Furthermore, the final copies have been examined by the director and the signature which appears below verifies the fact that any necessary changes have been incorporated, and that the thesis is now given final approval with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

May 23, 1967
Date

Magda B. Arnold
Signature of Adviser