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The Effects of Anxiety, Stress, and Competing Response Tendencies on the Learning of Verbal Concepts

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THE IMPORTANCE OF HIPPOCAMPAL REMNANTS IN DISCRIMINATION ABILITY

by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Out of more than 75 years of research and controversy on the hippocampus has come remarkable confusion. Our present state of misunderstanding may be given these categories, in order of increasing uncertainty: embryologic and phylogenetic development; structure; and function.

To avoid further confusion, let it be clear what is herein meant by hippocampus. Hippocampus is taken to include (in callosal animals) only that three-layered pyramidal archicortex, along with its precallosal and supracallosal remnants, which protrudes into some portion of the lateral ventricle (depending on phyletic position.) Dentate gyrus and subiculum will not be assumed under the term, hippocampus.

In acallosal animals, the hippocampus is seen to occupy a more anterior and dorsal position. But during phylogeny, the pressure dorsally from the mushrooming neocortex and ventrally from the corpus callosum has "squished" its anterior and dorsal portions leaving them vestigial in the eyes of most authors (Brodal, 1947; Zeman and Innes, 1963.) Simultaneously, the hippocampus proper was forced to fold in on itself and to assume a more and more ventrolateral position in the temporal lobe. The precallosal hippocampus, (also known as the anterior continuation of the hippocampus,) which comes to lie rostroventral to the genu of the corpus callosum, is said to be continuous with the anterior olfactory nucleus, perhaps by way of the medial olfactory striae (Crosby, 1962) and to extend uninterrupted around the genu as the supracallosal hippocampus (frequently termed the indusium griseum or hippocampal rudiment.) Johnson (Green, 1960) has made the additional assumption that the hippocampal primordium had an anterior extension which developed toward the main primordium (i.e., the hippocampus had 2 beginnings which grew toward one another) and thus allowed the corpus callosum to grow through the ensuing hippocampus, rather than "squish" it -- which assumption makes certain fiber connections more understandable.

The fimbria, which lies on the rostromedial surface of the hippocampus proper, is the main efferent fiber system from the hippocampus. As they course dorsorostrally, the fimbriae from both hemispheres join in the midline sending a substantial portion of fibers contralaterally as the hippocampal commissure. A few fibers of the fimbria swing up and around the splenium of the corpus callosum, and proceed rostrally for an undetermined distance as the longitudinal striae of Lancisi. Cajal (Brodal, 1947) noted these fibers but claimed they were afferent to the hippocampus proper. Some of these supracallosal fibers (perhaps bringing cortical association fibers with them) even penetrate the corpus callosum either to terminate in the septum pellucidum or to re-enter the fornix, which fornix is what the majority of fimbria efferents become. For, if the fimbria efferents do not decussate or course over the corpus callosum, then they proceed subcallosally forward without synapse as the body of the fornix, Here again, rostroventral to the hippocampal commissure, a good number of fibers cross forming the fornix commissure. Efferents that do not cross then either supply the septum pellucidum from the body of the fornix, or bend ventrally and in front of the anterior commissure to terminate in the septal nuclei as the precommissural fornix, or bend ventrally and behind the anterior commissure as the postcommissural column of the fornix, which courses straightway to the mammillary body. More recently, a large component of fornix fibers, presumably from the body of the fornix (Adey, 1951) has been described proceeding directly to the anterior thalamic nuclei without taking the more circuitous route through the mammillary body and mammillo-thalamic tract. Finally, there seem to be a few fornix fibers going directly to the preoptic region and habenula (Adey, 1951.)

Cajal (Brodal, 1947) has described three afferent fiber systems to the hippocampus. As mentioned above, he considered the supracallosal striae (of Lancisi) as afferent rather than efferent (both types of fibers may be present.) Secondly, fibers from the posterior cingulate gyrus (not the anterior) reach the hippocampus via the cingulum, probably coursing into the alveus.

And finally, the alveus itself brings the majority of afferents from the entorhinal and subicular regions.

Now, to add to the already complex state of affairs, Crosby (1962) summarizes recent evidence that the fimbria-fornix system is not solely efferent and that the alveus is not solely afferent. From the septal nuclei via the precommissural fornix and from the septum pellucidum via the body of the fornix, a great many afferent fibers reach the hippocampus and hippocampal gyrus. The alveus, which lines the entire ventricular aspect of the hippocampus, presents an even stranger picture, sending efferents both into the fimbria and back to the entorhinal and subicular areas.

The relevance of this complex but widely accepted anatomy of the hippocampus can best be studied and perhaps finally understood in a combined behavioral-physiological approach. Yet, no theorist has taken all of the above mentioned connections into account. Olds (1959) once stated amusingly but concisely: "The hippocampus changes function with each new experiment." A reflection of what he meant may be seen in the suggested functions several authors have put forth. In 1933, Herrick asserted that the hippocampus correlated diencephalic structures with cortical structures. Four years later, Papez spoke of the hippocampus as being part of an emotion circuit. Maclean (1949) elaborated upon Papez's idea hypothesizing that the hippocampus gathers all types of sensory impressions in mediating the autonomic aspects of emotion. Kaada (1951) and Issacson (1964) see the hippocampus as part of a forebrain suppressor system; Penfield and Milner (1958) and Nielsen (1958) see it involved in memory; Pribram (1961) claims it is particularly important in sequential activity. The most detailed formulation is that of Arnold (1960), who describes the hippocampus as part of a switching circuit mediating sensory, motor, and affective recall. She theorizes that the various portions of the hippocampal system subserve the various limbic areas, which in turn are connected with neighboring sensory and motor association areas. The hippocampal system picks up impulses from these limbic areas, which impulses run the hippocampal-fornix-mammillary body-midbrain-thalamic sensory nuclei-sensory association area circuit, thus mediating modality-specific recall. Accordingly, the lateral extent of the hippocampus proper would mediate auditory memory and the medial portion visual memory, while the supracallosal hippocampus would receive olfactory, motor, and tactual impulses at the approximate level of the genu, truncus, and splenium of the corpus callosum, respectively. Some of the foregoing notions are clearly developments of prior thought, while others are quite contradictory.

The purpose of this experiment is to lend some clarity to a confused picture of the hippocampus, by investigating several aspects of Arnold's theory. In detail, the effect on retention of a stage by stage bilateral ablation of the precallosal and supracallosal hippocampus is tested using a discrimination battery composed of 5 tasks: visual, auditory, olfactory, tactual, and motor (single alternation.) It is hypothesized that such lesions will prevent olfactory, motor, and tactual recall, but not visual and auditory recall. Prior studies investigating the supracallosal hippocampus have been deficient in several respects. Fagot (1962) found consistent olfactory deficits following interruption of the supracallosal hippocampus at the genu of the corpus callosum. However, he did not train his animals on non-olfactory tasks as a control procedure; thus the hypothesis of modality-specific memory was not properly tested. Furthermore, due to some very unfortunate circumstances, Fagot's slides were lost, thereby preventing additional analysis of the lesions. Neither did Gavin (1964) use any control discriminations when a few of her animals showed impaired alternation behavior following lesions in the supracallosal hippocampus along the truncus of the corpus callosum. Finally, Planek (1965) found no tactual or visual deficits with lesions over the splenium of the corpus callosum. Whether he might have found deficits in other modalities can only be answered by expanding the test battery.

CHAPTER II

METHOD

Subjects

Twelve naive male 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 400-500 grams. The temperament of the rats seemed in general to remain constant throughout the experiment.

Apparatus

Single Alernation: Training took place in a modified T-maze, consisting of a 8 inch x 8 inch x 8 inch start box, a 44 inch long runway leading from the start box to choice point, two 20 inch long arms leading in opposite directions from the choice point to 8 inch x 8 inch x 8 inch goal boxes, and 48 inch long return runways leading from the goal boxes straight back to the start box. All runways were 4 inches wide with walls on both sides 8 inches high. The entire maze was constructed of ½ inch plywood and was uniformly painted black. The start box had four doors: a hinged door on top through which the animal was placed into the maze and removed from the maze at the end of a day's training; one vertically-sliding door through which the animal exited on every trial; and two similar sliding doors which permitted re-entry from the two return alleys into the start box. These sliding doors were grooved on the bottom so as not to pinch the rat's tail and were operated via strings and pulleys. At a distance of three inches into both of the 20 inch arms leading from the choice point the rat encountered a one-way swinging door, through which he must push after he had made a choice, if he were to continue down the arm to the goal box. In both goal boxes, a perforated, vertically sliding metal door kept the animal from entering the return alley, on which door a magnetized dipper holding .3 cc. of water was found, if the animal's response had been correct. In this maze, the rats were required to make alternate right and left turns at the choice point in order to obtain a drink of water. A session consisted of ten trials per day and with an intertrial time of 15 seconds required 6-8 minutes per animal. The entire situation had been designed and run successfully so that the animal need never be touched during the session.

The following precautions had been taken to insure that the only relevant cues available to the animal would be movement-produced cues. To exclude visual cues from the choice point, the entire runway leading from start box to swinging doors beyond the choice point was covered with a layer of thick black paper over a layer of black cloth. In addition, the room was completely darkened except for a ten watt photographic-red light source suspended above the maze. Also, the start box was illuminated with a small 18 watt white light source which kept the animal light-adapted between trials, but was turned off before the animal was allowed to exit from the start box. Possible auditory cues were masked by white noise emanating from a 6 inch x 9 inch speaker mounted midway over the runway leading from the start box. The following intensities of white noise were thus provided at the following points: 86 decibels in the start box; 86 decibels at the choice point; 72 decibels in the goal boxes. Whatever tactual and olfactory cues may have been present should have been constant from trial to trial and regardless of whether the animal turned right or left, because there was but one choice point and the maze was uniformly constructed of the same material. Isaacson (1964) has suggested that rats alternate to the olfactory cues provided by their own trail; if this is so, it was his experimental design that allowed it. For, his rats ran only two trials per day and could quite reasonably have distinguished the path they had taken before. Our rats ran ten trials per day, traversing the same path every 45-60 seconds. It is doubtful that even a rat can distinguish the freshness of trials laid down 45 seconds apart. Besides, based on the performance of 15 ocularly enucleated rats that were run thousands of trials in developing this maze, it may safely be stated that the rat has decided upon leaving the start box which way he is going to turn, as is obvious in the arc in which he travels. (Incidentally, trimming off the vibrissae seemed to have no effect on their performance.) However, the olfactory-cue notion was nonetheless put to the test by repainting the entire choice point overnight between sessions. Subsequently, the rats did no better and no worse.

Olfactory Discrimination: Training took place in a 15 inch long x 8 inch high x 4 inch wide compartment made of ½ inch plywood and painted black. The hinged top door was made mostly of wire mesh; the front side where a 4 inch wide x 3 inch long x 2½ inch high wood trough with sliding cover was permanently located, was made of glass, in order to observe the animal. Through the trough was slid manually a 40 inch long x 1½ inch wide x 3/4 inch high wood tray, in which were embedded ten #7 metal thimbles, spaced evenly at intervals of three inches along the tray. The same five thimbles always each held 1½ cc. of lemon-water solution; the same other five always held 1½ cc. of vanilla-quinine solution -- their relative sequence in the tray being determined be a table of random numbers. The stimulus solutions themselves both had the same very slight yellow coloring and except for their odors were indistinguishable.

Rats soon learned to drink the lemon solution and refuse the vanilla. Sessions consisted of ten trials per day, each thimble being presented one at a time and only once; starting position on the tray for the first trial and direction of movement of the tray were likewise randomized. With an intertrial interval of 15 seconds, a session lasted for about five minutes.

Visual Discrimination: Training took place in small-animal test chambers #1102TCM1, each within its own sound-proof cubicle, manufactured by the Foringer Company of Rockville, Maryland. The test area approximated a 10 inch cube, was made of aluminum, and had a stainless steel grid floor. A single bar protruded into the chamber, which bar when depressed at the right time actuated a dipper bringing .1 cc. of water up through the floor, or when depressed at the wrong time delivered a shock to the hind feet of the animal. The shock had the following parameters: 80 volts a.c.; .32 milliamperes; .2 second duration. To keep the conditions of reinforcement constant, the water was always fresh; and the grid floor was scoured daily. The visual stimuli were provided by two small 4.75 watt lights, which either flashed at a rate of six per second or remained on constantly. The animal was never in total darkness, in order to exclude possible cues from eye muscles at the onset of light. Even though the chambers were supposed to be sound-proof and were kept closed during running, it had been positively observed that the sounds coming from the programing equipment and from neighboring test chambers provided definitely usable auditory cues to the animals. Thus, the equipment and the test chambers had been located in different rooms. Furthermore, 82 decibels of white noise was piped into each test chamber through a 2 inch loudspeaker located in its rear wall.

Programing and data recording were completely automatic. Randomly varying intervals of flashing light alternated with randomly varying intervals of steady light; the rat could get water only when the lights were flashing. A session lasted 15 minutes.

Auditory Discrimination: Training took place in the same apparatus as described under Visual Discrimination above. Alternate periods of clicking and silence replaced flashing versus steady light. Clicks with an intensity of 68 decibels (as measured from within the test chambers) came at a rate of six per second from a 6 inch x 9 inch speaker mounted on the wall 6 feet from the test chambers. Of course, there was no attempt to suppress any auditory cues. Thus, no white noise was used; and the test chambers remained open one inch, to allow the sound to enter. The reason for using a speaker mounted on the wall rather than the 2 inch speakers in the test chambers was that the latter produced vibratory cues which even deaf animals could use to successfully negotiate this discrimination (data to be published.)

A session which lasted 15 minutes was, however, run in total darkness.

Tactual Discrimination: The apparatus used was again the same as described under Visual Discrimination above. However, neither visual nor auditory cues were available (i.e., no lights, no clicking, chamber closed, white noise on.) Instead, the animal had to probe his way through the session; he had to keep testing the bar to see whether he would get water or shock. The rat learned to press rapidly when water was available and to slow down when he felt a shock to his hind feet. That this indeed comprised 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 was significantly lower than with shock, $p = .001$. Under the circumstances herein described, most rats probed with shock at an accuracy of 60-70% correct.

A session lasted 15 minutes.

Procedure

Training: Under conditions of 24-hour water deprivation and ad lib access to food, the rats were trained on all discriminations to a very high degree of accuracy -- an average of 90% correct responses over three successive days (refer to the preceeding paragraph for the reason why the tactual discrimination must be an exception.) Once the animals mastered all discriminations, they were sated and given the first in a series of 14-day rest periods, all of which terminated in 48 hours of water deprivation. The 48-hours deprivation comprised the last two days of a 14-day rest period. Then the animals underwent the first in a series of

5-day retention periods, 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. 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 rest period between R_1 and R_2, the animals received various precallosal and supracallosal hippocampal lesions. R_3 was given to disclose any delayed effects that the lesions might have, and to re-establish a base level against which R_4 would be compared. R_4 was run after a series of second operations was performed; any animal suspected of having a deficit after the first operation was not given a second operation. The statistical analysis used to determine deficits was a _t_-test between each animals preoperative and postoperative scores. This was judged to be the best way to control for individual differences in ability and in lesion placement. In addition to being water deprived 48 hours before the start of all retention periods, the animals were weighed daily. Intra-animal weights varied less than 2% across retention periods.

Operations: The animals were anesthetized by placing them in a 4-liter chamber, into which a gaseous mixture of ether and air was pumped. After 2 minutes of the ether treatment, the animals were given a .20 cc. intraperitoneal injection of Nembutal, followed by a few more minutes of ether, if necessary. Clean surgical technique was used, consisting of shaving the animal's head and then washing it with alcohol, incising the scalp in the midline, scraping the periosteum, boring trephine holes with a dental drill fitted with #2 round burrs, and inserting .046 inch in diameter electrodes coated with Formvar except for a 1 mm. tip exposure. A spray antiseptic and suture clips were used to close the wound. Lesions were made with a Grass Radiofrequency Lesion Maker, Model Lm-3, and monitored with a Knight milliammeter. For precallosal lesions, monopolar electrodes (with the animal serving as a ground) were placed bilaterally 4 mm. before the bregma, .5 mm. lateral, and 6 mm. deep. For supracallosal lesions, bipolar electrodes were placed 2 mm. apart in the midline, the front (hot) electrode being either 1 mm. before the bregma and 3.6 mm. deep for anterior lesions or 3.5 mm. behind the bregma and 3.2 mm. deep for posterior lesions. A current of 15 milliamperes for 10 seconds was used in all lesions. During the operation, the rat remained fixed in a Krieg-Johnson stereotaxic apparatus, which had been modified to preclude the use of earplugs. It has been found that earplugs permanently and totally deafen up to 50% of the animals operated on, which animals usually exhibit extremely disoriented and spastic behavior arising from inner ear destruction, and occasionally starve themselves to death (data to be published.)

Histology: The animals were sacrificed and perfused with isotonic saline and 10% formalin. Their brains were extruded, trimmed, left in 10% formalin for 2-4 weeks, mounted in paraffin, and cut at 5 microns thickness. Serial sections of the lesion sites were stained with Luxol fast blue (for cell bodies and myelin) and a modified Nauta stain (for non-myelinated fibers and possible degeneration.) Slides were read by the author and confirmed by Dr. Stanley Jacobson, neuropathologist at V. A. Research, Chicago.

CHAPTER III

RESULTS

The results of this study fall into three categories: 1.) data pertinent to the specific hypothesis being tested; 2.) incidental findings concerning the hippocampal commissure and operation trauma; and 3.) the phenomenon of refusals or "freezing" behavior.

Table 1 is a summary of animals, operations, tissue damage, deficits, and refusals.

Tables 2, 3, 4, 5, and 6 represent the statistical analysis of all the preoperative versus postoperative running data. As is immediately apparent from the tables, the hypothesis concerning the role of the precallosal-supracallosal hippocampal system in the retention of olfactory, motor, and tactual memories must be rejected. In fact, the destruction of this system produced no deficits of any kind. However, the unintentional destruction of the hippocampal commissure and transection of the superior fornix in animal #16 produced significant and predicted deficits in olfaction and alternation.

Table 7 was prepared as a brief summary statement of the experiment. It is derived from the data of all the animals except

#16's olfactory and alternation scores. Total predicted deficits were determined on the following bases: Visual and auditory deficits should be the same as probing without pre-response discriminative stimuli, which is precisely what the tactual discrimination was. Tactual deficits should be the same as probing without shock. Olfactory and alternation deficits were the mean scores of animals in our lab which have actually had deficits. Thus, all predicted deficits had an empirical basis. Some notions on operation trauma are likewise included in Table 7.

Finally, there were postoperatively several incidences of refusal in the alternation maze, and in the olfactory apparatus. In such cases, the conditions of refusal were noted in detail and the retention periods continued otherwise intact. At the conclusion of a given 5-day retention period in which there were refusals, the animals involved were kept on deprivation and made to rerun the discriminations they refused for as many sessions as they refused. Some of this make-up running was done with the animals at a slightly greater deprivation level (13-15% loss in body weight rather than the usual 9-12% loss,) and is so indicated in the Appendix, pp. 38-44, along with the other details of refusal. In every instance, the animals then performed normally and very accurately (not significantly different from their preoperative scores, as pointed out in the tables.)

Table 1

SUMMARY OF HISTOLOGICAL AND BEHAVIORAL DATA

The lesions fall generally into three categories, with additional or lesser damage indicated in the table (see Figure 1):

A---Bilateral destruction of the precallosal hippocampus and dorsal anterior olfactory nucleus. The mean cross-sectional area of these spherical lesions was 1.00 mm.^{2}.

B---Bilateral ablation of the caudal half of the anterior cingulate cortex, with minimal damage to the adjoining medial frontal and premotor cortex. The size of these cigar-shaped lesions averaged 2.3 mm.^{2} in cross-sectional area by 3 mm. in length; they were all too shallow to transect the supracallosal hippocampus at this point.

C---Bilateral ablation of the rostral half of the retrosplenial cortex, with little bilateral damage to the cingulum and complete transection of the supracallosal hippocampus at this point. The average lesion size in this case was 2.1 mm.^{2} in cross-sectional area by 2.4 mm. in length.

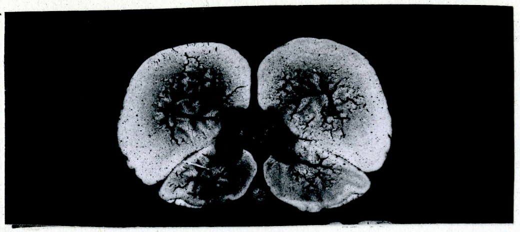
Rat #	Oper. #	Lesion	Additional Description	Deficit	Refusal
4	1*	A	unilateral.	-	-
10	1**	A	mainly damage to cingulum and cingulate cortex.	-	3-day olf.
2	1	A		-	2-day motor
	2	C		-	5-day motor 3-day olf.
9	1	A		-	-
	2	C		-	-
5	1**	B		-	5-day motor
11	1	B		-	-
	2	C		-	-

Table 1 (con't)

Rat #	Oper. #	Lesion	Additional Description	Deficit	Refusal
12	1	B	unilateral section of supracallosal hippocampus.	-	-
	2	C		-	-
13	1	B	mostly unilateral.	-	-
	2	C	unilateral damage to visual cortex.	-	-
16	1**	C	minimal damage to cortex; complete transection of corpus callosum, superior fornix, and hippocampal commissure.	olf. motor	-
7	1	C	unilateral damage to visual cortex.	-	1-day motor
	2	B	slightly unilateral.	-	5-day motor
14	1	C	too shallow for supracallosal hippocampus.	-	-
	2	B	slightly unilateral.	-	1-day motor
15	1	C		-	-
	2	B		-	1-day motor

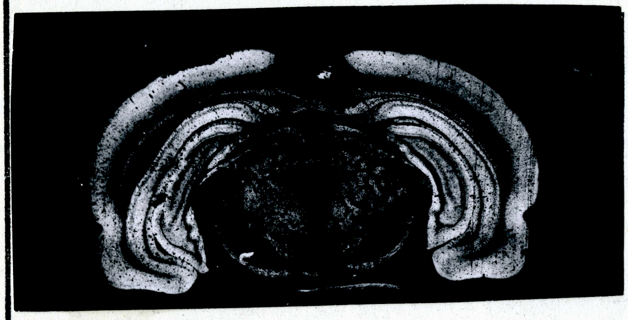
* Died in second operation.

** Suspected of having a deficit, and therefore did not receive a second operation.

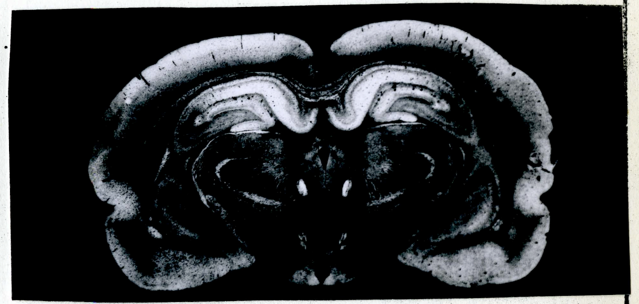


Type A
Animal 2

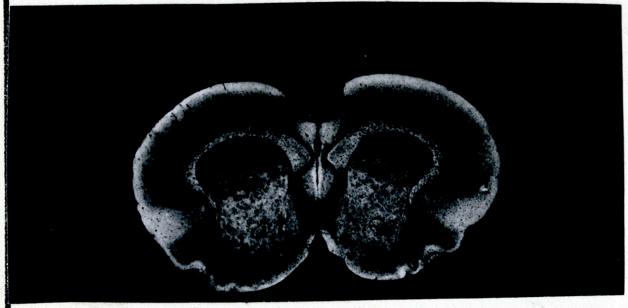
Type A, unilateral
Animal 4



Type C
Animal 11



Type C, shallow
Animal 14



Type B
Animal 5

Animal 16

Fig. 1. Photographs* of slides depicting each of the lesion types described in Table 1 and the hippocampal commissure-superior fornix lesion of animal #16.

*A note of thanks to Mr. Raymond A. Gross for his knowledge, skill, and time in preparing these photographs.

Table 2

VISUAL DISCRIMINATION DATA
A COMPARISON OF PREOPERATIVE AND POSTOPERATIVE PERFORMANCE IN TERMS OF PERCENTAGE CORRECT OF TOTAL RESPONSES

Rat #	Oper. #	Mean Scores in Retention Periods				S.D.^{a}	t^a
		R_1	R_2	R_3	R_4		
2	1	94.6	90.8	-	-	3.70	2.30
	2	-	-	94.4	89.4	9.41	1.19
4	1^b	93.4	91.2	(97.4)	-	4.66	1.06
5	1^c	96.2	90.4	(97.4)	(97.6)	9.78	1.33
7	1	99.2	98.0	-	-	2.78	0.97
	2	-	-	98.0	98.8	1.30	1.37
9	1	96.8	95.6	-	-	3.27	0.82
	2	-	-	98.0	99.6	0.89	4.00*
10	1^c	93.8	87.6	(96.2)	(99.2)	11.50	1.20
11	1	95.6	98.0	-	-	3.51	1.53
	2	-	-	98.0	96.6	4.04	0.78
12	1	92.4	90.8	-	-	7.70	0.46
	2	-	-	96.6	93.6	3.32	2.02
13	1	96.4	94.4	-	-	4.47	1.00
	2	-	-	96.0	93.6	3.65	1.76
14	1	93.4	94.4	-	-	3.16	0.71
	2	-	-	95.6	94.4	3.77	0.71
15	1	94.6	94.4	-	-	5.54	0.08
	2	-	-	95.0	95.8	7.46	0.24
16	1^c	93.6	89.8	(95.4)	(93.8)	6.38	1.33

* $p. = .01$, but change is in the wrong direction; the animal improved after the operation.

---

[a] These are based on matched variables, and thus computed between pairs of corresponding sessions. N - 1 = 4 degrees of freedom.

[b] Died in second operation, but did run R_3.

[c] Suspected deficit; no second operation; but did run R_3 & R_4.

Table 3

AUDITORY DISCRIMINATION DATA
A COMPARISON OF PREOPERATIVE AND POSTOPERATIVE PERFORMANCE IN TERMS OF PERCENTAGE CORRECT OF TOTAL RESPONSES

Rat #	Oper. #	Mean Scores in Retention Periods				S.D.[a]	t[a]
		R_1	R_2	R_3	R_4		
2	1	96.2	93.0	-	-	8.17	0.88
	2	-	-	89.8	89.4	6.73	0.13
4	1[b]	94.6	88.0	(92.0)	-	11.06	1.34
5	1[c]	94.4	87.2	(92.6)	(93.4)	7.56	2.13
7	1	94.6	97.4	-	-	3.27	1.91
	2	-	-	93.4	94.2	2.59	1.56
9	1	94.2	93.0	-	-	3.35	0.80
	2	-	-	95.4	95.6	3.42	0.13
10	1[c]	95.8	95.2	(90.4)	(95.8)	1.34	1.00
11	1	93.6	95.0	-	-	3.44	0.91
	2	-	-	93.2	90.4	14.55	0.43
12	1	93.0	89.2	-	-	5.26	1.62
	2	-	-	94.2	87.8	6.47	2.21
13	1	93.6	93.6	-	-	4.64	0.00
	2	-	-	94.0	89.6	7.54	1.30
14	1	96.8	93.0	-	-	3.35	2.54
	2	-	-	96.8	94.2	4.78	1.22
15	1	90.8	91.4	-	-	3.78	0.36
	2	-	-	88.8	88.0	7.46	0.24
16	1[c]	91.8	85.6	(90.2)	(88.8)	10.33	1.34

[a] These are based on matched variables, and thus computed between pairs of corresponding sessions; N-1= 4 degrees of freedom.

[b] Died in second operation, but did run R_3.

[c] Suspected deficit; no second operation; but did run R_3 & R_4.

Table 4

TACTUAL DISCRIMINATION DATA
A COMPARISON OF PREOPERATIVE AND POSTOPERATIVE PERFORMANCE IN TERMS OF PERCENTAGE CORRECT OF TOTAL RESPONSES

Rat #	Oper. #	Mean Scores in Retention Periods				S.D.[a]	t[a]
		R_1	R_2	R_3	R_4		
2	1	68.6	64.2	-	-	4.11	2.07
	2	-	-	61.4	56.8	7.70	1.34
4	1^b	72.4	60.2	(70.8)	-	9.36	2.91 <.05
5	1^c	70.0	63.4	(64.2)	(60.6)	6.62	2.23
7	1	71.3	66.7	-	-	12.90	0.63
	2	-	-	72.2	67.6	12.90	0.81
9	1	68.4	64.8	-	-	6.69	1.20
	2	-	-	66.6	69.0	11.78	0.46
10	1^c	60.0	54.0	(58.0)	(63.2)	9.67	1.39
11	1	56.8	52.0	-	-	7.12	1.51
	2	-	-	47.8	51.0	10.23	0.70
12	1	56.6	58.2	-	-	3.85	0.93
	2	-	-	58.2	56.0	5.72	0.86
13	1	73.2	67.0	-	-	2.87	4.35* <.05
	2	-	-	66.4	58.6	7.95	2.19
14	1	72.4	70.4	-	-	6.93	0.64
	2	-	-	68.0	66.0	4.90	0.91
15	1	52.8	55.2	-	-	10.26	0.52
	2	-	-	52.6	54.6	7.97	0.56
16	1^c	54.8	53.2	(53.8)	(61.2)	5.32	0.67

* Three degrees of freedom, due to equipment malfunction on one test day.

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[a] These are based on matched variables, and thus computed between pairs of corresponding sessions. N - 1 = 4 degress of freedom.

[b] Died in second operation, but did run R_3.

[c] Suspected deficit; no second operation; but did run R_3 & R_4.

Table 5

OLFACTORY DISCRIMINATION DATA
A COMPARISON OF PREOPERATIVE AND POSTOPERATIVE PERFORMANCE IN TERMS OF PERCENTAGE CORRECT OF TOTAL RESPONSES

Rat #	Oper. #	Mean Scores in Retention Periods R_1	R_2	R_3	R_4	S.D.[a]	t[a]
2	1	98.0	94.0	-	-	15.17	0.06
	2	-	-	98.0	96.0*	4.47	1.00
4	1[b]	96.0	98.0	(100.0)	-	10.95	0.41
5	1[c]	96.0	84.0	(98.0)	(88.0)	14.83	1.81
7	1	100.0	94.0	-	-	8.94	1.50
	2	-	-	98.0	98.0	7.07	0.00
9	1	100.0	94.0	-	-	5.48	2.45
	2	-	-	98.0	98.0	7.07	0.00
10	1[c]	100.0	74.0*	(78.0)	(92.0)	20.74	2.80 $<.05$
11	1	98.0	92.0	-	-	5.48	2.45
	2	-	-	100.0	100.0	0.00	0.00
12	1	96.0	98.0	-	-	8.37	0.54
	2	-	-	100.0	96.0	8.94	1.00
13	1	98.0	98.0	-	-	0.00	0.00
	2	-	-	98.0	100.0	4.47	1.00
14	1	100.0	98.0	-	-	4.47	1.00
	2	-	-	100.0	100.0	0.00	0.00
15	1	96.0	98.0	-	-	8.37	0.54
	2	-	-	100.0	98.0	4.47	0.00
16	1[c]	98.0	58.0	(56.0)	(98.0)	17.32	5.16**

* Some of the sessions that this mean is based on were make-up sessions.

** $p = .005$

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[a] These are based on matched variables, and thus computed between pairs of corresponding sessions. $N - 1 = 4$ degrees of freedom.

[b] Died in second operation, but did run R_3.

[c] Suspected deficit; no second operation; but did run R_3 & R_4.

Table 6

MOTOR (ALTERNATION) DISCRIMINATION DATA
A COMPARISON OF PREOPERATIVE AND POSTOPERATIVE PERFORMANCE IN TERMS OF PERCENTAGE CORRECT OF TOTAL RESPONSES

Rat #	Oper. #	Mean Scores in Retention Periods R_1	R_2	R_3	R_4	S.D.[a]	t[a]
2	1	75.5	77.8*	-	-	16.28	0.30
	2	-	-	77.8	82.2*	16.72	0.59
4	1[b]	88.9	84.4	82.2	-	14.74	0.67
5	1[c]	93.3	77.8*	(88.9)	(86.7)	9.79	3.50 <.05
7	1	91.1	84.4*	-	-	16.72	0.88
	2	-	-	84.4	80.0*	20.02	0.49
9	1	91.1	66.7	-	-	19.69	2.75*
	2	-	-	88.9	77.8	20.57	1.20
10	1[c]	91.1	77.8	(80.0)	(80.0)	18.04	1.63
11	1	66.7	84.4	-	-	12.54	3.14 <.05
	2	-	-	80.0	70.0	25.74	0.95
12	1	86.7	80.0	-	-	16.72	0.88
	2	-	-	86.7	77.8	14.30	1.37
13	1	88.9	77.8	-	-	15.51	1.58
	2	-	-	84.4	75.5	12.10	1.63
14	1	80.0	86.7	-	-	14.74	1.00
	2	-	-	66.7	91.1*	18.04	2.99 <.05
15	1	88.9	73.3	-	-	21.45	1.60
	2	-	-	91.1	71.1*	27.39	1.62
16	1[c]	86.7	**	**	80.0	21.45	0.69**

* Some of the sessions that this mean is based on were make-up sessions.

** #16 ran but never alternated during R_2 or R_3 (rf. pp. 30-31.) R_1 is compared to R_4 to show that he recovered.

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[a] These are based on matched variables, and thus computed between pairs of corresponding sessions. N - 1 = 4 degrees of freedom.

[b] Died in second operation, but did run R_3.

[c] Suspected deficit; no second operation; but did run R_3 & R_4.

Table 7

MEAN SCORES,
IN TERMS OF PERCENTAGE CORRECT OF TOTAL RESPONSES,
DURING THE VARIOUS RETENTION PERIODS
ON THE VARIOUS DISCRIMINATIONS
FOR ALL ANIMALS EXCEPT #16

Discrimination	Learning* Criterion	Predicted** Total Deficit	R_1	R_2	R_3	R_4
Visual	90.0	60.0	95.0	93.0	96.5	95.6
Auditory	90.0	60.0	94.1	91.8	92.6	91.7
Olfactory	90.0	50.0	98.0	92.9	97.1	96.6
Tactual	60.0	46.1	66.1	60.8	61.7	60.4
Alternation	88.9	42.2	85.5	80.0	83.3	80.0

* The average for three consecutive days.

** As explained in the text, page 18, all of these scores were empirically determined.

Note -- All retention periods (R_1, R_2, R_3, R_4) are separated by 14 days of rest. The rest periods separating R_1 from R_2 and R_3 from R_4 were both begun by placing brain lesions in the animals, as specified in the *Procedure* section. Thus R_2 and R_4 are postoperative retention periods, which it will be noticed, are characterized by slight depressions in scores, as compared to preoperative retention periods. The depression, due to operation trauma, does not always accompany brain lesions; but it did occur in 70% of the cases in this study, and perhaps should be expected this often under similar conditions. The average loss in accuracy due to the first operation was approximately 4.04%; the average loss due to the second operation was approximately 1.38%. According to the *t*-tests performed on each animal individually, such losses were in no case significant. Furthermore, none of the depressed scores at all resembled the predicted total deficits; nor did they (except for alternation scores) ever dip below the rigid criterion which all animals met in the learning phases of the project. (The difficulties with the alternation maze are discussed in the Appendix.) However, in terms of an animal-by-animal nonparametric analysis, using the Wilcoxon matched-pairs signed-ranks test, the trauma of the first operation tended to be significant: $p = .02$ for visual; $p = .05$ for auditory; $p = .05$ for olfactory; $p = .01$ for tactual. Very strangely, such traumatic effects did not even tend to be significant for the second operation. Finally, the loss in accuracy was not due merely to the 14 days of rest which coincided with the operations, because rest alone between R_2 and R_3 seemed to improve the animals' accuracy, or at least return it to preoperative levels.

What this all means is that the chances are about 70-30 that the first brain surgery an animal undergoes will tend to produce a slight transient loss in discrimination accuracy. If the experiment is well controlled and the experimenter knows what kinds of performance changes to expect, such losses will not be misconstrued as deficit due to specific brain sites destroyed. To the author's knowledge, a similar trauma phenomenon has been seen in every brain-lesion study conducted in the Behavior Laboratory, regardless of lesion site and size. As a finding in this study, it must be viewed as tentative and incidental to the specific hypothesis being investigated. It has been discussed here only to point to the existence of a problem that should be thoroughly studied.

CHAPTER IV

DISCUSSION

It has been observed that, after having been trained extensively in the alternation maze, more than 6% [1] of the normal intact animals would occasionally refuse to run this task. Thus, it is not unreasonable to find some operated animals occasionally refusing, also. Yet the mere fact that both intact and lesioned rats exhibit refusals is insufficient in itself to dismiss the whole problem. The question of why still remains. Certainly, brain damage may be a factor in some cases of refusal in some studies; but such an explanation seems unlikely in this study. Instead, among the answers turned up by investigating the refusals of the operated rats in this study, some provide likewise adequate answers for intact refusals: extinction, lack of thirst, and startle. But some of the answers are pertinent only to animals that have been through the rigor of an operation: sore head from a scalp wound, and conditioned emotional reaction to being placed in anything resembling the

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[1] This figure would be more on the order of 12-15% if all experimenters had noted such occurrences in writing. Unfortunately, the one experimenter in charge of most of the alternation-maze running did not take notes and could not recall frequency of refusal.

ether chamber. Thus, it is also reasonable to expect even more frequent refusals from operated animals. Naturally, one tries to avoid such things as refusals; but if they happen and can be explained as suggested above, then one simply admits that accidental, chance variables have crept into his study. Under such conditions, it would be neither realistic nor parsimonious to look for an explanation in terms of brain damage. (The Appendix deals in detail with each case of refusal.)

Animal 16, whose entire hippocampal commissure was destroyed and superior fornix transected, but with minimal damage to overlying cortex, exhibited the only real retention deficits of the experiment. His postoperative olfactory scores were precisely what would be expected of a total deficit; he drank from every cup indiscriminately. This deficit remained for seven weeks (3 rest periods and 2 retention periods) until the third postoperative retention period when he suddenly recovered completely. The fact that such recoveries can occur points to a real need for longitudinal studies. Why such recoveries take place can only be answered by further investigation of the brain. It is certainly possible that the hippocampal commissure and/or the superior fornix may contain many but not all of the fibers necessary for the utilization of olfactory memories. This notion must be tested. Animal 16's alternation deficit was even stranger. Unlike other animals that have been deficient in this task (3-4 alternations per 10 trials), animal 16 never alternated; instead he always ran to one side. Since such repetition was not rewarded and since the animal would not run to the other side of the maze, he would extinguish each day before completing a session. It seems he simply forgot that he ever turned left before. However, he did not refuse; he did not forget how to run the maze; and he did not forget which way he turned last, since he always went the same way. Thus, to say he had a deficit in alternation and could not remember which way he turned last is incorrect; rather, he had amnesia for part of a previously learned response pattern. When during the third postoperative retention period (R_4) the animal was once again "informed" that there were two possible turns he could make (by forcing 4 trials to the left), the animal began alternating on his own. After one session he was once again alternating perfectly. To call this relearning would perhaps cloud the issue even more. For it is doubtful that he would have overcome the deficit without help; and once the help was given, he required but one-tenth the time other animals require to master the task.

As for the neural structures that this study specifically investigated, the precallosal hippocampus and the posterior 3 mm. of the supracallosal hippocampus above the splenium of the corpus callosum seem not to be involved in the retention of visual, auditory, tactual, olfactory, and motor tasks. These results are a two-fold extension of Planek's negative findings that much smaller transections of the supracallosal hippocampus above the splenium did not affect the retention of tactual and visual tasks. First of all, Planek conjectured that perhaps the supracallosal fibers that penetrate the corpus callosum are sufficient to enable tactual recall, and that is why he found no deficits. Now, regardless of the direction that supracallosal hippocampal fibers run, the large (3 mm.) lesions of this study certainly, in addition, transected any fibers penetrating the posterior truncus and the splenium of the corpus callosum. Thus the posterior 3 mm. of the supracallosal hippocampus and any penetrating fibers at that point are of no consequence to the recall of tactual memories. Secondly, this study added auditory, olfactory, and motor tasks to the test battery Planek used, and additionally failed to find any impairment.

Again concerning the involvement of penetrating fibers, it is a curious fact that Fagot and Gavin were not bothered by them in their studies which showed olfactory and motor deficits respectively. Their lesions were far too small (1 mm.) to do anything but transect the supracallosal hippocampus. Thus, if we accept their results, then the importance of penetrating fibers with regard to olfaction and alternation should also be rejected -- and this presents a problem. If the supracallosal hippocampal fibers run posteriorly along the top of the corpus callosum, then according to Arnold's formulation olfactory and motor, as well as tactual recall, should have been impaired by posterior lesions (which animals #2, 7, 9, 11, 12, 13, 14, and 15 received). If the fibers run anteriorly, then lesions in the precallosal hippocampus should have impaired these behaviors (animals #2 and 9, their first operations). If the fibers run both ways, then introducing both lesions in the same animal should have produced deficits (animals #2 and 9, combination first and second operations). None of these possibilities was supported in this study. Thus, if Fagot's and Gavin's findings are not to remain a puzzle, the precise nature of their deficits must be determined -- which is in fact a topic currently under study.

In conclusion, concerning the precallosal-supracallosal hippocampal system, there is more evidence against than for its involvement in the psychological activities described by Arnold. However, as was incidentally discovered, perhaps an investigation of the superior fornix would have proved more fruitful in supporting her theory. Her psychological analysis remains among the most credible; and her notion of one neural circuit mediating sensory-specific memory retrieval is still the most interesting notion to date on the subject. Its value lies in its economy and also in that it affords us, with our meager knowledge of the brain, at least a plan of attack centered around known circuits. The cingulum, the hippocampus proper-fornix system, and the longitudinal bundle of Probst, which is suspected of running the length of the corpus callosum, should be future targets.

CHAPTER V

SUMMARY

Twelve male albino rats received various lesions in the precallosal-supracallosal hippocampal system, in order to assess the importance of this system in the recall of visual, auditory, tactual, olfactory, and motor (alternation) tasks. In order to use each animal as his own control, the following design was used: initial training to a high criterion on all tasks; rest; retest; rest and operation; retest; rest and optional second operation; retest. The results were negative, thereby strongly indicating that this system does not participate, alone at least, in the retention of the above-mentioned behaviors. The only significant changes in behavior came from a misplaced lesion which severed the hippocampal commissure and superior fornix and disrupted olfactory and motor recall. However, the precise and verified importance of these structures must await future experimentation.

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APPENDIX

When an animal refuses to run a well-learned discrimination, one wonders whether the animal has forgotten what he was supposed to do, whether he can no longer discriminate, whether he is now frightened, or whether the incentive for performance is no longer sufficient. As an explanation for the refusal behavior seen in this experiment, no one alternative will suffice. Each animal was a case in himself, and will thus be discussed separately. In this way, the author hopes to make clear his reasons for viewing all of the present cases of refusal as accidental occurrences.

#2 -- On a few occasions in the preoperative training and retention periods, animal #2 hesitated for 2-3 minutes before leaving the start box in the alternation maze. As compared to most of the other animals, this behavior was unusual and already indicative of what might be called a dislike for the maze. He refused to run on days 3 and 4 of R_2, the first postoperative retention period. However, he ran normally on days 1, 2, and 5 of R_2 and throughout R_3, on which occasions, according to body weight, he was no thirstier.

During R_4, he urinated daily in the maze and completely refused to run. His three days of olfactory discrimination refusal were accompanied by the same signs of emotion. So it seems the #2's emotional condition worsened with each operation. Seven other animals received two operations, #9 having the same damage as #2; yet no other animal showed signs of emotion. Thus, neither the operations _per se_ nor the tissue damage appear to be the aggravating factor.

However, there was something unique about #2's first operation, that may well have made it for him subsequently unpleasant to be confined in a small enclosure such as the start box of the alternation maze or the olfactory apparatus itself. Briefly, to get #2 into the ether chamber and keep him there proved to be quite a problem. During the course of the struggle, much emotion was displayed by both rat and man. It is suspected that being placed into the two test apparati is similar enough to being placed in the ether chamber to cause #2 to freeze. In all of the author's experience, this was the only time such an operative difficulty occurred. Thus, a comparison with other animals so treated cannot be made. Yet the judgment that is the best explanation and that therefore his refusals were accidentally caused has been made, especially in light of the fact that under slightly greater deprivation (3-4% greater loss in body weight), the animal ran normally.

#5 -- On the first day of postoperative running (R_2), in the alternation maze, animal #5 appeared very confused and stopped running after making 6 mistakes. He continued refusing to run the maze for the remainder of R_2. According to body weight, when at the conclusion of R_2 this animal underwent make-up sessions, (which he ran without hesitation) he was no more thirsty than he was on the first day of R_2. During R_3 and R_4, which he ran normally, he was even less thirsty than in R_2. Thus, thirst seems not to have been a factor involved in the refusals. Of the seven animals that received lesion type B, animal #5 suffered by far the least extensive damage. Thus, neural damage seems also not to have been a factor. If there can be an explanation for his early postoperative refusals, it might best run as follows. Certainly, #5 did extinguish on the first day of R_2, when after 6 errors he stopped running. If extinction is really learning something new, then #5 learned there was no longer any water reward to be had in the maze. #16, as discussed elsewhere, extinguished similarly. However, #5 showed no spontaneous recovery until the make-up sessions following R_2, which he ran normally, as he did all of R_3 and R_4. Moreover, the first day of a 5-day retention period has always been a rather bad day for most rats running the alternation maze. And this stands to reason, since retention periods are spanned by 14 days of rest (and perhaps some forgetting.) In fact, on this task the mean score on the 1st day of a retention period for 82 normal, intact animals is 76.7% correct (with a range of

44.4-100%) which is considerably below the learning criterion of 90% correct. Thus, that #5's 1st day of R_2 was simply a "bad" one is quite tenable. But, unlike other rats, #5 made his errors consecutively, and quit.

#7 -- Why animal #7 refused to run on day 1 of R_2 will never be known. For without any coaxing he finished R_2 and ran R_3 normally. But, why this animal seemingly refused to run all 5 days of R_4 is known. Unlike some of the other animals, the slightest increase in deprivation during the make-up sessions did not make him run. In fact, severe deprivation was likewise ineffective. Investigation showed that on a given trial, animal #7 would leave the start box immediately, travel the runway, turn at the choice point, and stop at the one-way swinging doors. He either would not or could not push through them. The animals usually push through these doors with their heads, and it seems that his head might still have been tender from the second operation. Of course, that he simply did not remember how to push through is another alternative, although a less likely one since attempts at retraining were useless. The purpose of the swinging doors was two-fold: 1.) primarily to prevent the animals from retracing; and 2.) added insurance that the choice point be void of visual cues. However, since the maze room itself was totally darkened, it was safe to rerun #7 holding both swinging doors open until he made a choice.

Under these conditions he ran normally.

#10 -- This animal refused to run the olfactory task the last 3 days of R_2. He always took a drink or two at the beginning of the session but then behaved as though he were no longer thirsty. When in the make-up sessions he was made slightly thirstier, he discriminated quickly and accurately. However, under the usual deprivation regimen, he did run normally in R_3 and R_4. It seems that he just wasn't thirsty enough on those occasions which he refused.

#14 -- The only instance in which this animal refused was on day 3 of R_4 in the alternation maze. He was thirstier on days 1 and 2 and less thirsty on days 4 and 5. Thus thirst seems not to have been a factor. Day 3 was just one of those days, which even intact animals on occasion have. Of all the intact animals ever run in this maze, 6.1% have "refused" on one or more days for undeterminable reasons.

#15 -- On the last day of the last retention period (R_4), #15 refused to run the alternation maze. This is best explained by the fact that toward the end of the session on the previous day, this rat was frightened (as indicated by his crouching and urinating in the goal box) by a very loud noise made by a workman in the adjoining room. A day's rest was sufficient to dissipate his fear; he ran his make-up session normally.

It would have been a grave error and impossible task to force a single explanation upon these diverse cases of refusal. Had running notes not been taken on each animal in addition to numerical scores, the temptation to explain refusals in terms of brain damage would have been the sole alternative. In fact, such an attempt was made, but its unworthiness was immediately apparent. For each of the three lesion sites seemed to produce refusals, but only in some of the animals that received such lesions and only occasionally in most of those animals that did refuse. In this author's opinion, the honest and workable solution lay in a thorough scrutiny of the experimental situation.

The question still arises as to why refusals appeared only in alternation and olfactory tasks, and not in visual, auditory, and tactual ones. Concerning the alternation task, the answer has many probable facets. To begin with, the total water reward for running the maze was far smaller than that given in all the other tasks. Moreover, after drinking the water on a given trial, the animals had to run away from the reward part of the maze in order to position themselves for the next trial; the animals did this reluctantly. The required discrimination was the most difficult of the five used, as evidenced by the length of time necessary to learn the task initially, the variability of day-to-day performance once learned, and the tendency of the animals during the rest periods to forget the alternation task more readily than the other tasks. (This last notion, of difficulty, is reflected in Table 7 by consistently sub-criterion means achieved by the animals in the various retention periods -- a characteristic found only in the alternation task.) In other words, because it was difficult, perhaps less rewarding, and in general more open to fortuitous happenings, the alternation maze invited refusals, even in intact animals. However, all the refusers eventually ran the maze, and ran it normally. Thus, the relevant memories and the retrieval circuits were still intact.

As for the olfactory refusals, they are best seen as fear arising from similar and unpleasant past experience (#2), and insufficient thirst (#10).

APPROVAL SHEET

The dissertation submitted by Victor L. Dufour has been read and approved by 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.

May 31, 1967
Date

Magda B Arnold
Signature of Adviser