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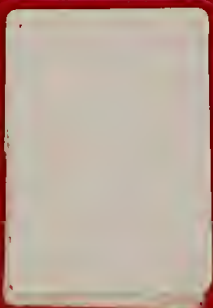
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EFFECT OF MAMMILLOTHALAMIC TRACTOTOMY ON UNNATURAL
APPETITIVELY MOTIVATED AVOIDANCE BEHAVIOR IN RAT

A Thesis Presented

By

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Submitted to the Graduate School of the
University of Massachusetts in
partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

June 1972

Major Subject: Psychology

EFFECT OF MAMMILLOTHALAMIC TRACTOTOMY ON UNNATURAL
APPETITIVELY MOTIVATED AVOIDANCE BEHAVIOR IN RAT

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ACKNOWLEDGMENT

To my dear friend and adviser Professor E. E. Kriekhaus I wish to express my deepest appreciation and gratitude for all the help and encouragement he has given me throughout this study. His unique understanding of the beauty and complexity of the brain within a comparative neurophenomenological framework has been inspiring and stimulating, and the influence of his ideas in the development of my own appreciation of the wondrous and mysterious workings of the psyche has been immense. From the study of our evolutionary predecessors to that of man, I stand as a child in awe not only of the complexity, beauty and oftentimes incomprehensibility of experience but also of the possibilities of human experience as yet little explored.

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In all mammalian species thus far studied, it is well established that the large, prominent, mammillothalamic tract (MTT) of the mammalian forebrain, with nearly as many fibers as the optic nerve, connects the phylogenetically primitive mammillary bodies to the uniquely mammalian anterior thalamic nuclei (Fry, et al., 1963; Fry et al., 1964; Guillery, 1961). This tract is thus interposed between hippocampus, many of whose projections terminate in the mammillary bodies, and the cingulate cortex, which receives fibers from the anterior thalamus. In contrast to the morphological prominence of the mammillothalamic system, which is seen upon even gross examination of the mammalian brain, knowledge of the function of this system is relatively limited.

The only behavior that appears to be affected by destruction of the mammillothalamic tract in mammals, specifically cat and rat, is acquisition and retention of "unnatural" avoidance behavior in situations involving danger (Thomas, Fry, Fry, Slotnick and Kriekhaus, 1963; Kriekhaus, 1964, 1965, 1969a; Kriekhaus and Chi, 1966; Kriekhaus and Lorenz, 1968; Kriekhaus, Coons, Greenspoon, Weiss, and Lorenz, 1968). But acquisition or retention of "natural" avoidance behavior in cat or rat in situations involving danger is unaffected by mammillothalamic tractotomy (Kriekhaus, 1964, 1966, 1969a, 1969b). Thus mammillothalamic tractotomy produces a decrement in avoidance behavior in situations which involve "unnatural" behavior and danger but no decrement in performance in

situations involving "natural" behavior and danger. It is not behavior in dangerous situations that is being affected by MTT lesions since the animal's performance would be impaired regardless of whether the task involved "natural" or "unnatural" behavior. The immediately obvious question, then, is whether "unnatural" behavior alone or "unnatural" behavior only in dangerous situations is affected by mammillothalamic tractotomy.

"Unnatural" avoidance behavior is characterized by the animal's having to give up, so that he can avoid punishment, a primitive, unlearned, stereotyped response in order to initiate a newly learned one, a response very low in his response hierarchy. For example, an animal's response patterns which are innately high in his response hierarchy to danger are freezing, fleeing or fighting. In an unnatural avoidance task such as one which requires an animal to press a lever in order to avoid being shocked, fighting would obviously be inappropriate and maladaptive, fleeing is blocked and the animals therefore freeze. Since freezing results in the animal's getting shocked, this response also becomes unquestionably maladaptive for the organism. The task is considered to be an unnatural one because the animal must learn to inhibit this freezing response, which is high in his response hierarchy to the present danger, and initiate a newly learned one (pressing a lever) which is very low in his response hierarchy, so that he can avoid pain. Thus, pressing a lever to avoid shock while locked in a box in which the animal receives foot shock is very unnatural,

while running or jumping out of this box, responses which are high in the animal's response hierarchy to pain, is very natural. The theory further postulates that the more unnatural the task confronting an animal in a dangerous situation, the smaller the animal's subjective probability that flight behavior will lead to safety since ultimately there is no exit from the dangerous situation; and thus the balance between flight and freezing will be tipped more in favor of freezing, a situation which will be manifested in an absence of the avoidance response. It appears, therefore, that at least in the case of dangerous situations, the animal's ability to initiate novel forms of behavior is critically dependent on the suppression of innate, primitive response patterns which are high in the animal's response hierarchy--a function which the previous data suggests could be dependent on the integrity of the mammillothalamic system.

Thus, is unnatural behavior of animals with MTT lesions a necessary and sufficient condition to produce a decrement in avoidance performance or must danger also be involved? The present experiment attempted to answer this question by investigating the effects of MTT lesions on avoidance performance in a situation involving unnatural appetitively motivated behavior. Although several previous studies involving appetitively motivated tasks have demonstrated that natural avoidance behavior in cat and in rat is also unimpaired by MTT lesions, it is

unclear what effect mammillothalamic tractotomy might have on unnatural appetitively motivated avoidance behavior (Thomas et al., 1963; Kriekhaus, 1966; Kriekhaus et al., 1968; Kriekhaus and Jones, 1968; Kriekhaus and Lorenz, 1968; Kriekhaus and Randall, 1968; Kriekhaus, 1969c, 1969d). The task used in this study requires a rat to give up a presumably stereotyped and primitive pattern of behavior (drinking water when thirsty) to initiate a newly learned one (pressing a lever), a response low in his response hierarchy, in order to avoid the water's being shut off.

METHOD

Subjects consisted of 22 male albino rats of the Sprague-Dawley strain from the Holtzman breeding laboratories, and were approximately 90-120 days old when the experiment began.

The training apparatus consisted of a small animal plexi-glass chamber enclosed within a sound insulated cubicle with part of the door made of one-way glass. General illumination was supplied by a 28-volt bulb located on the rear wall of the outer chamber. A water bottle was located outside of the apparatus from which plastic tubing from the bottle to a spout

within the testing chamber was interrupted by a solenoid valve attached to the outer wall of the intelligence panel. Onset and termination of the water flow could thus be achieved by means of activating or deactivating the solenoid valve. A retractable lever was positioned below and just to the right of the water spout. One light located above the lever was illuminated simultaneously with the onset of a 600cps tone of low intensity, presented through a speaker on the rear wall of the sound-proof chamber, which served as a compound warning signal for the termination of water flow in the avoidance training.

At the beginning of the experiment each rat was deprived of water for approximately 23 hrs 45 min and subsequently maintained on this deprivation schedule for the duration of the experiment. Each subject was first pretrained with a shaping technique to press the lever to receive 5 sec of water for each lever press. Pretraining continued until the rat's lever pressing to receive water reached a stable base-line rate. This was accomplished in approximately 5-7 days. Following this period avoidance training began. At the beginning of each trial the rat was allowed to have water for 5 sec which was followed by the onset of the tone and the cue light over the lever. If the rat did not press the lever within 10 sec following the onset of the tone and light three things happened simultaneously: the water flow was terminated, the house light went out, and the lever was retracted for 30 sec. During this "blackout"

period the warning signals remained on but because of the withdrawal of the lever, the animals were unable to press the lever. At the end of this 30 sec period the house light was re-illuminated and the lever was reinstated so that if the rat then pressed the lever he would terminate the warning signals and again make water available. If, however, the rat pressed the lever during the 10 sec between the onset of the warning signals and the scheduled withdrawal of the lever and termination of the water flow, he would temporarily avoid the termination of the water flow, terminate the warning signals and would enjoy water for 5 sec before the warning signals were again activated. Also, if he pressed the lever before the onset of the warning signals, the timer was immediately recycled to the beginning of the trial, where the water was again made available for 5 sec. Thus, if the rat pressed the lever at any time, this response was always followed by a reinforcing set of events, i.e., the trial was immediately recycled to the 5 sec free water period.

Each animal was tested for 20 trials per day. On the day after he reached a relatively consistent and stable rate of avoidance responding for approximately 4 days, lesions were produced electrolytically by means of a stereotaxically aimed electrode. Surgical and histological procedures were the same as those described previously (Kriekhaus, 1965). Lesions were intended to transect the MTTs bilaterally.

Following surgery and a recuperative period of approximately 1 week, a 3-day postoperative retention phase of the experiment began. The procedure for this period was identical to that followed during the acquisition phase described above. At the conclusion of the experiment each animal was sacrificed and its brain prepared for histological verification of lesion placements.

RESULTS

Following histological examination of brain tissue, the animals were divided into three groups on the basis of the amount of destruction of the MTT. Careful inspection of tissue damage indicated that the lesions were not uniform in size and shape between animals. The breadth and height of each lesion was measured microscopically. The four measurements (two for each lesion) were summed for each rat, and then were averaged over the individual rats in the three groups: complete MTT lesions (mean=5.8mm), partial MTT lesions (mean=3.2mm), and no MTT lesions (mean=2.8mm). Although there was a statistically significant difference in lesion size among the three groups, there was no significant correlation between lesion size and changes in behavior

($r=.18$, $p<.25$). Extra MTT damage was randomly distributed about the MTT, and again there were no detectable relationships between changes in behavior and extra MTT damage.

Evaluation of the rates of preoperative learning indicated that the mean number of days to reach a stable and consistent base-line rate of avoiding for approximately 4 days was very similar for all three groups. Likewise, the number of avoidances out of a possible total of 60 avoidances (20 trials/day for 3 days) for the 3 days just prior to surgery, as indicated in column 3 of Table 1, was quite similar for all three groups. Additional detailed preoperative perform-

Table 1 about here

ance for the 3-day period just prior to surgery is presented in Tables A-1 and A-2 of the Appendix. The data in both Tables A-1 and A-2 is categorized according to the schema employed for Tables 1 and 2 presented here.

Although there was considerable variability in postoperative performance, it is clear from column 4 of Table 1 that there was no material difference in the 3-day postoperative performance among the three groups. The mean number of avoidances out of a possible total of 60 for animals with complete MTT lesions was 19.1; for animals with partial MTT lesions, 14.0; and for animals with no MTT lesions, 16.6. Indeed there was a tendency for animals with MTT lesions to do

TABLE 1

Preoperative and Detailed Postoperative Avoidance Performance

Rat No.	%MTT destroyed	Total Pre-op	Total Post-op	MODE		TIME	
				Leave Post-op	Reach Change	Before Post-op	After Post-op
832	100,100	43	12	12	-6	0	12
840	100,100	42	41	5	1	23	18
833	100,100	41	42	20	-5	20	22
821	100,100	37	9	0	-26	5	4
839	100,100	37	6	1	2	3	3
831	100,100	36	17	0	-19	13	4
837	100,100	31	36	32	-13	8	28
828	100,100	27	7	0	-7	2	5
826	100,100	16	2	1	-6	0	2
Mean		34.4	19.1	7.8	-8.7	8.2	10.8
876	40,0	40	12	0	-19	2	10
877	30,97	37	19	1	-19	10	9
830	75,0	37	8	8	-19	1	7
834	75,100	32	17	0	6	15	12
870	100,0	31	11	0	-20	7	4
874	40,90	30	22	3	-9	7	15
836	5,55	26	9	0	-13	4	5
Mean		32.8	14.0	1.7	-13.3	6.5	8.8
875	0,0	44	7	4	-5	4	3
873	0,0	43	43	6	-6	18	25
823	0,0	39	8	8	-4	2	6
825	0,0	37	3	0	-6	1	2
871	0,0	31	34	14	-7	14	20
835	0,0	26	5	2	-23	3	2
Mean		36.6	16.6	5.6	-8.5	7.0	9.6

slightly better! Although there was a marked reduction in the number of avoidances postoperatively, it is clear from examination of columns 2, 3 and 4 of Table 1 that this drop was independent of whether or not the MTT was destroyed. The level of postoperative avoidance performance for those animals, regardless of group, who avoided the water's being shut off significantly less postoperatively than preoperatively was equivalent to about the 3rd or 4th day level of avoidance performance of the initial acquisition period. The average number of avoidances for these animals on the 3rd or 4th day of acquisition was 3.1 and for the 3-day postoperative period, 3.2 avoidances.

In addition, avoidances were dichotomized according to whether a) the rat inhibited his drinking and left the water tube prior to pressing the lever ("leave mode"), or b) the rat did not inhibit his drinking but merely reached down to press the lever while he was drinking ("reach mode"). Although the animals could solve this task by utilizing either mode of response, it is the "leave mode" that is actually the test of whether unnatural behavior of animals with MTT lesions is a necessary and sufficient condition to produce a decrement in avoidance performance since it involves the inhibition of an innate, stereotyped response and the initiation of an unnatural, learned one in order to avoid the water's being shut off. Behaviorally, these two modes of responding were easily distinguishable. An avoidance was

recorded in the "leave mode" when the animal stopped drinking, moved his head away from the water tube and then pressed the lever. If he merely continued to drink and simultaneously reached over with his paw to press the lever, the avoidance was scored in the "reach mode." Even though the "reach mode" seems to be a much less demanding and more efficient strategy for keeping the water available, within each group of animals there was a sufficient number of avoidances in the "leave mode" to test the above question.

Preoperatively, 36% of the total number of avoidances for all animals were scored in the "leave mode" and postoperatively, 31% were recorded in this mode. Although there was a slight but non-statistically significant difference between the overall preoperative and postoperative percentage of avoidances in the "leave mode", this difference was due primarily to the performance of the animals with partial and no MTT lesions. The preoperative and postoperative percentage of avoidances in the "leave mode" for animals with complete MTT lesions was 42% and 41% respectively.

When considering these and the other categories into which the avoidances were grouped, the question arises whether to use the postoperative performance score or the change score (i.e., the quantitative change in performance from the preoperative to the postoperative condition). In the case of the "leave mode", since there was no significant correlation between the preoperative and the postoperative performance

($r=.22$, $p<.25$), the change score would not be an appropriate index of performance for analysis because it includes both preoperative and postoperative variability. Therefore the postoperative performance measures were used, and these are presented in column 5 of Table 1. Again, these values represent the number of avoidances out of a possible total of 60 avoidances. Although an analysis of variance indicated that there was a difference among the groups approaching significance ($F=9.4$, $df=2$, 19 , $p<.10$), upon closer examination of the data it became obvious that this difference was due primarily to the postoperative performance of the animals with partial MTT lesions. It can be seen that there was no material difference in the number of avoidances between animals with complete MTT lesions (mean=7.8) and those with no MTT lesions (mean=5.6) but a marked difference between these animals and those with partial MTT lesions (mean=1.7). Since the performance of the animals with partial MTT lesions was collectively much worse than the performance of those with complete and no MTT lesions, the effect of mammillothalamic tractotomy upon postoperative avoidance behavior, at least in the "leave mode", appears negligible.

In the "reach mode" there was a significantly high correlation between the preoperative and postoperative avoidance performance ($r=.73$, $p<.001$). Thus the change score presented in column 6 of Table 1 was a more appropriate measure of

performance, since it takes into account both the preoperative and postoperative levels of performance. There was no significant difference among the three groups on this measure.

The number of postoperative avoidances out of a possible total of 60 avoidances were further dichotomized on the basis of whether they occurred a) prior to the onset of the warning signals (before), or b) following the onset of the warning signals (after). There was no significant correlation between the preoperative and postoperative performance in either the "before" ($r=.31$, $p<.10$) or "after" ($r=.23$, $p<.25$) condition; therefore the postoperative score was used. It is clear from columns 7 and 8 of Table 1 that in the "time" category there were again no significant differences among the three groups in either the "before" or "after" categories.

Latencies were originally recorded for avoidances that occurred both before and after the onset of the warning signals. Since there was not even a suggestion of a difference between the latencies of the before and after conditions within all the groups, both mean latencies for each animal were summed to provide one representative measure for the avoidance latency. Although there was a slight (mean=.4 sec) but non-statistically significant increase in avoidance latency from preoperative to postoperative performance in both the before and after conditions, this increase was almost identical for both the MTT and control groups. Since the preoperative to postoperative correlation for the combined avoidance

latency conditions was $r=.28$, $p<.10$, the postoperative performance measure (in sec) was used. As can be seen from column 3 of Table 2, there was no significant difference among

Table 2 about here

all three groups in their avoidance latencies.

The only other difference among the three groups which approached significance occurred in their escape latencies as indicated in column 4 of Table 2. It took somewhat longer for the animals with complete MTT lesions to press the lever after it had been reinstated following the "blackout" period than animals with no MTT lesions ($t=1.53$, $p<.10$). Column 10 represents postoperative performance measures (in sec) since the preoperative to postoperative correlation was quite low ($r=.28$, $p .10$).

DISCUSSION

The animals in the present experiment were required in an appetitively motivated task to give up a presumably primitive, innate, stereotyped response (drinking water when very thirsty) and initiate a newly learned one (pressing a

TABLE 2

Postoperative Avoidance and Escape Mean Latencies

Rat No.	% MTT destroyed	Avoidance Post-op	Escape Post-op
832	100,100	-	1
840	100,100	7	1
833	100,100	6	1
821	100,100	3	5
839	100,100	5	2
831	100,100	4	3
837	100,100	7	2
828	100,100	6	3
826	100,100	-	4
Mean		5.4	2.4
876	40,0	7	1
877	30,97	6	1
830	75,0	5	2
834	75,100	6	1
870	100,0	5	1
874	40,90	7	1
836	5,55	6	1
Mean		6.0	1.1
875	0,0	6	2
873	0,0	7	2
823	0,0	6	2
825	0,0	5	1
871	0,0	6	1
835	0,0	5	1
Mean		5.8	1.5

lever) in order to avoid the water's being shut off. The results indicate that in such an unnatural situation, the retention of this appetitively motivated avoidance behavior, at least in rat, appears unaffected by mammillothalamic tractotomy. There is no indication that the animal's ability to leave the water tube, regardless of whether he actually stopped drinking and left the tube in order to press the lever or merely reached over to press the lever while still drinking, is affected by MTT lesions; this is an important finding in elucidating the function of the mammillothalamic system.

If the MTT does play a role in a system which "...tips a balance away from primitive and stereotyped response patterns which are innately high in the animal's response hierarchy", as hypothesized earlier (Kriekhaus, 1967) it would appear from the results of the present study that this applies only to the realm of avoidance behavior in unnatural situations involving danger. Thus unnatural behavior of animals with MTT lesions seems to be necessary but not sufficient to produce a decrement in avoidance performance. The task used in this experiment is a good task for testing the validity of the above hypothesis in a situation involving unnatural appetitively motivated avoidance behavior because like tasks previously used in aversive situations (Kriekhaus and Lorenz, 1968; Kriekhaus et al., 1968), it is one in which a) there is competition between the innate stereotyped responses and

unnatural learned ones, b) the animals must learn to inhibit these primitive innate kinds of responses and initiate a newly acquired response in order to receive and maintain reinforcement, and c) high motivational and emotional levels characterize the task.

In relation to the above general characteristics of an unnatural situation let us look at the "thirst" motivated task in a way similar to that of the task involving "fear" discussed in the introduction to this study. As stated previously, an animal's innate response patterns to danger are freezing, fleeing or fighting. In an unnatural avoidance task such as the lever-press shock avoidance, the animal must learn to suppress his freezing response, which is the strongest in his response hierarchy because there is no exit from the dangerous situation, and initiate an unnatural learned response, pressing a lever, in order to avoid being shocked. Likewise, an animal's innate response patterns to thirst are exploring (locomotion), ingesting, or manipulating. Once the rat knows where the water is located his innate response to thirst in such artificial laboratory situations is to ingest. In fact in the present study at the onset of the warning signals typically the animals' drinking would rapidly increase apparently in anticipation of the water's being shut off. Thus this appetitive situation is considered to be an unnatural one because it requires the animal to inhibit the well-learned stereotyped response of drinking when thirsty, a response

high in his response hierarchy to thirst, and initiate an unnatural learned one, a response low in his response hierarchy, in order that he can avoid the termination of the water flow.

The unnaturalness of this appetitive situation was reflected in the animal's difficulty in the learning of the task. Approximately 20% of the total number of animals initially included at the beginning of the study were discarded prior to surgery due to their inability to achieve a stable and significantly elevated base-line rate of avoidance responding. The mean base-line rate of avoidance responses prior to surgery for all animals included in this study out of a possible maximum of 20 avoidances on any given day was itself fairly low--11.5 avoidances with a range of from 6 to 15. In addition, the acquisition of a relatively consistent and stable rate of avoidance responding was achieved, on the average, in a lengthy 14 days. On those trials when the animals did not avoid the water's being shut off, typically they would still elicit behaviors that would appear to indicate some awareness of the impending "punishment." They would tenaciously cling to the water tube, the head would rotate about 45 degrees, the hind portion of the body would struggle toward the lever and licking would increase slightly. If we can infer from these behavioral indices that all the important sensory associations have been made and appear to

be present, we can conclude that these animals know well the contingencies but at times find it difficult, both before and after surgery, to suppress their drinking and press the lever in order to avoid the termination of water flow. The results of a previous pilot study, although flawed by some minor problems inherent in its design, also demonstrated the degree of unnaturalness of the task even during the acquisition period --no animal in this pilot study was ever able to reach a reasonable and consistent level of avoidance responses. In fact, in this previous study the average number of avoidances, either preoperatively or postoperatively, for an animal on any given day was in every case less than 1. It is thus highly unlikely that the task used in the present experiment is not unnatural enough or did not involve a primitive enough response. The lack of any suggestion of a decrement both in avoidance behavior and in avoidance latency in this task with MTT lesions demonstrates that the retention of unnatural appetitively motivated avoidance behavior appears not to be dependent on the integrity of the mammillothalamic system.

Although escape performance is theoretically and conceptually different from avoidance performance, the escape performance of the animals in the present study is somewhat of an anomaly. The escape latencies for animals with complete MTT lesions were somewhat longer than the escape latencies for animals with no MTT lesions. The overall increase in escape latencies occasioned by MTT interruption which has been

reported earlier (Kriekhaus and Lorenz, 1968; Kriekhaus and Randall, 1968; Kriekhaus and Jones, 1968) is difficult to interpret. First, the decrement, which merely approached statistical significance, was not large, and second, in no case were the lesions confined to the MTT. Such a non-specific decrement could have been accounted for by the larger lesions in the group with complete MTT lesions. In addition, given the lack of effect of mammillothalamic tractotomy on rates of pressing a lever for milk in cat (Kriekhaus, 1966; Kriekhaus and Lorenz, 1968) and the lack of effect on running speed in rat in a variety of other kinds of appetitive tasks (Kriekhaus et al., 1968; Kriekhaus, 1969c) suggests that the mammillothalamic system probably has little or no direct effect on motivation in an appetitive task, although this problem must be further explored.

In spite of the possible limitations in the results of this study attributed to a) the non-accountable overall drop in postoperative avoidance performance, and b) the significant amount of variability in the animals' performance, the lack of any detectable difference among the groups except in their escape latencies, makes it reasonable to consider that, at best, there could be only a small effect of MTT lesions which is masked by this variability. The extent of the variability in both the pre- and postoperative avoidance performance and the postoperative latencies is reflected in Figures 1 and 2 respectively.

Figures 1 and 2 about here

That the unnaturalness of the task confronting a rat or cat determines the severity of the decrement in avoidance behavior following MTT lesions appears from the present results and others (Kriekhaus, 1967) to be specific only to situations involving danger. The importance of the hypothesized role of the mammillothalamic system in mediating the balance between stereotyped and novel behavior does not account for this discrepancy between "fear" motivated and appetitively motivated situations. However, this discrepancy can best be understood from a phylogenetic point of view.

Kriekhaus (1967) has eloquently pointed out the great biological significance of the mammillothalamic system to mammals. The most advanced extant reptiles have little or no hippocampus and fornix, only poorly differentiated mammillary bodies, no identifiable MTT, and poorly developed or nonexistent anterior thalamic nuclei. On the other hand, even the most primitive mammals possess a relatively well developed mammillothalamic system and this system reaches its greatest prominence in man. Mammals, particularly primates, have been successful because of their ability to initiate novel, non-stereotyped responses and to appreciate the outcome of this behavior. The primary goals of survival and propogation of

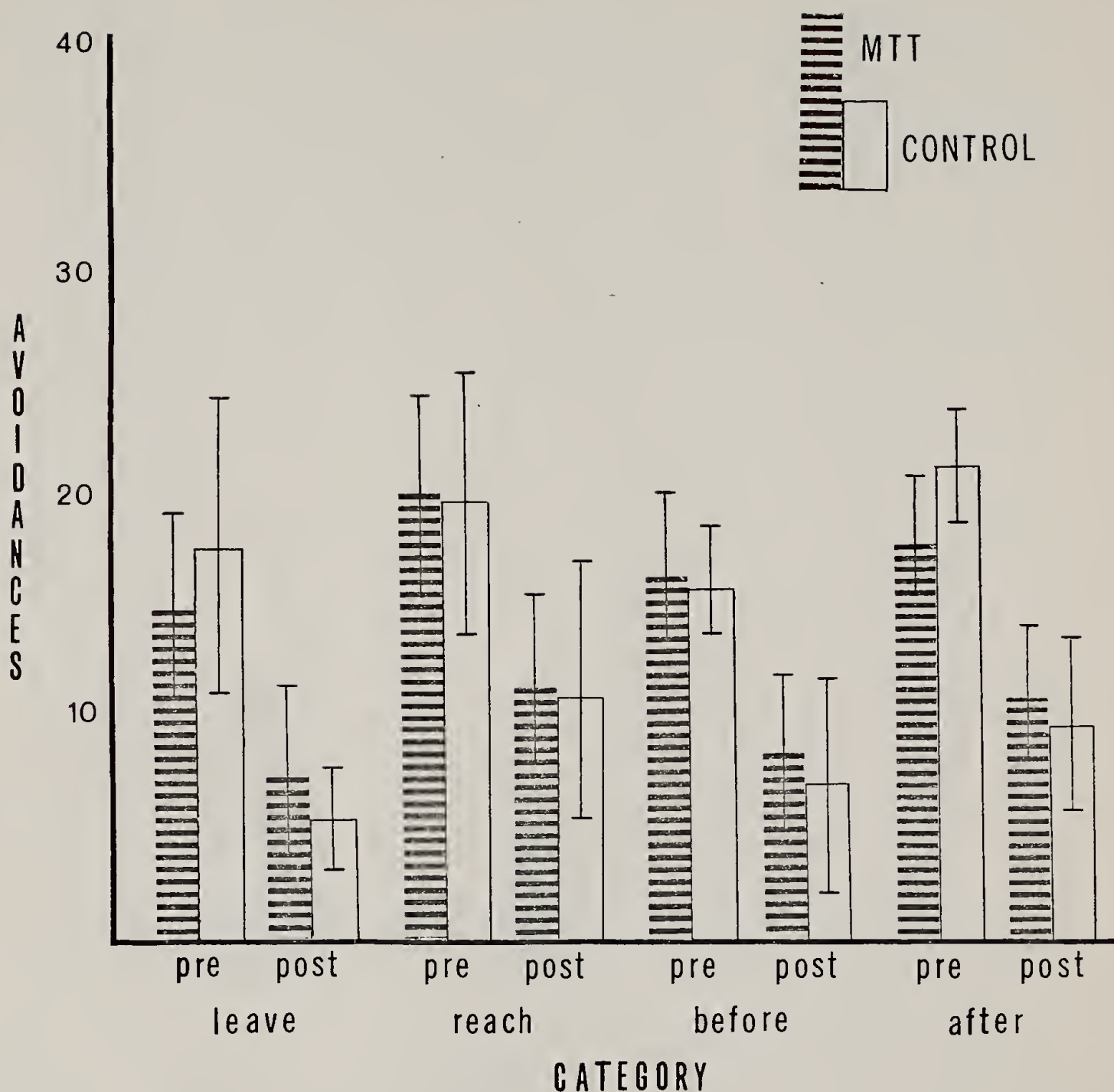


FIG. 1. Preoperative and postoperative avoidance performance for animals with complete MTT lesions (striped) and no MTT lesions (solid). Each bar represents the group's mean avoidance score and standard error of the mean for the 3-day period just prior to surgery and the 3-day period after surgery. Avoidances are categorized according to "mode", leave and reach, and "time", before and after.

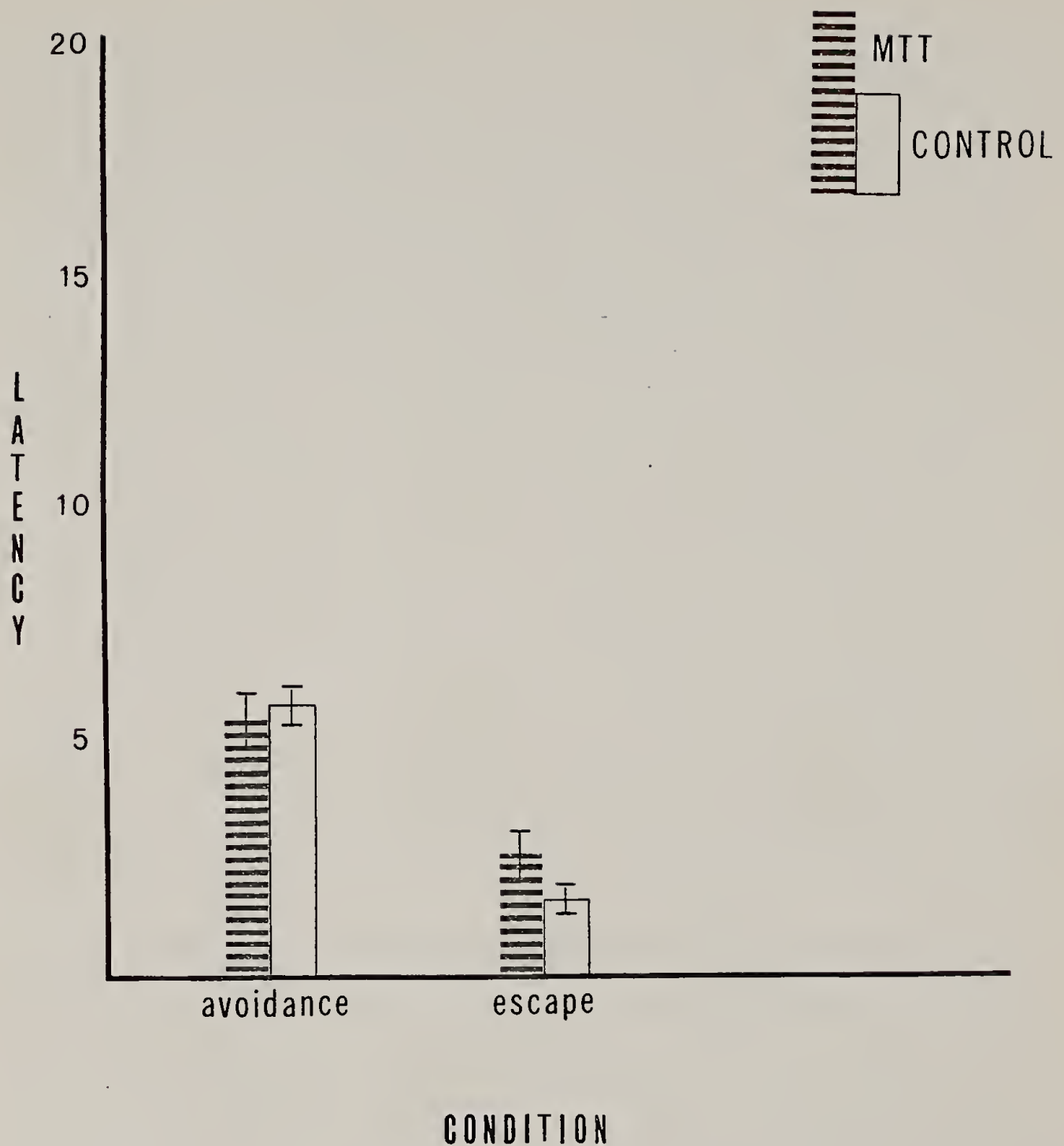


FIG.2. Postoperative avoidance and escape latencies for animals with complete MTT lesions (striped) and no MTT lesions (solid). Each bar represents the group's mean latency and standard error of the mean (in sec) for the 3-day period following surgery.

a species are in part a function of the ability of a species to escape from predators, to minimize the probability of being detected by predators, to protect themselves from the harshness of the elements, etc., activities relentlessly involving imminent danger or the pervasive threat of danger or harm to the species. Thus, given the overwhelming presence of danger in the animal's natural habitat, it would seem that a biological system that would play an important role in tipping the balance away from primitive and stereotyped response patterns would undoubtedly be selected for and find expression and usefulness in situations involving danger. This is not to imply that such a system would be specific only to dangerous situations. On the contrary, these results indicate that there probably are separate biological systems for withdrawal (aversive realm) and approach (appetitive realm) behavior. Schneirla (1959) presents much phylogenetic and ontogenetic evidence demonstrating that in all animals the species-typical pattern of behavior is based upon biphasic, functionally opposed mechanisms insuring approach or withdrawal reactions. Through evolution, higher psychological levels have arisen in which through ontogeny such mechanisms can produce new and qualitatively advanced types of adjustment to environmental conditions. Although the plasticity of higher animals has been attributed to the development of the neocortex and its associated subcortical mechanisms, at least in the case of dangerous situations it appears

that the animal's ability to initiate novel forms of behavior is also critically dependent on the suppression of innate, primitive response patterns which are high in the animal's response hierarchy--a function apparently dependent on the integrity of the mammillothalamic system.

Derangement of memory, disruption of autonomic and endocrine functions, and decrements in conditioned avoidance behavior have all been reported following destruction of either the mammillary bodies or the MTT. The sizable quantity of this literature notwithstanding, other studies utilizing similar lesions in the mammillothalamic system have found no suggestion of any of these deficits except those involving unnatural avoidance behavior. The contradictory and confusing literature implicating lesions of the mammillary bodies in memory derangements such as the Korsakoff syndrome, and the literature implicating the mammillary bodies in autonomic and endocrine regulation, has been reviewed elsewhere (Barbizet, 1963; Krieckhaus, 1962). In relation to avoidance behavior, the present results reiterate what is now appearing to be the crucial question concerning the role of the mammillothalamic system on behavior--namely, why is only unnatural avoidance behavior in dangerous situations affected by interruption of this system?

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APPENDIX TABLES

- A-1 Detailed Preoperative Avoidance Performance
- A-2 Preoperative Avoidance and Escape Mean Latencies

TABLE A-1

Detailed Preoperative Avoidance Performance

Rat No.	% MTT destroyed	Days to Learn	MODE		TIME	
			Leave Pre-op	Reach Pre-op	Before Pre-op	After Pre-op
832	100,100	13	37	6	5	38
840	100,100	10	7	35	19	23
833	100,100	11	14	27	26	15
821	100,100	13	2	35	31	6
839	100,100	17	34	3	8	29
831	100,100	16	0	36	31	5
837	100,100	13	14	17	11	20
828	100,100	14	13	14	13	14
826	100,100	17	10	6	5	11
Mean		13.7	14.5	19.8	16.5	17.8
876	40,0	12	9	31	14	26
877	30,97	11	0	37	20	17
830	75,0	13	18	19	21	16
834	75,100	15	11	21	9	23
870	100,0	12	0	31	22	9
874	40,90	11	2	28	10	20
836	5,55	16	1	22	19	4
Mean		12.8	5.8	27.0	16.4	16.4
875	0,0	9	36	8	7	37
873	0,0	10	0	43	14	29
823	0,0	23	35	4	12	27
825	0,0	23	28	9	19	18
871	0,0	10	4	27	19	12
835	0,0	21	0	26	24	2
Mean		16.0	17.2	19.5	15.8	20.8

TABLE A-2

Preoperative Avoidance and Escape Mean Latencies

Rat No.	% MTT destroyed	Avoidance Pre-op	Escape Pre-op
832	100,100	5	1
840	100,100	5	1
833	100,100	6	1
821	100,100	3	2
839	100,100	5	1
831	100,100	4	1
837	100,100	6	1
828	100,100	4	1
826	100,100	4	1
Mean		4.6	1.1
876	40,0	5	1
877	30,97	5	1
830	75,0	4	1
834	75,100	7	1
870	100,0	5	1
874	40,90	5	1
836	5,55	3	1
Mean		4.8	1.0
875	0,0	6	1
873	0,0	5	2
823	0,0	6	2
825	0,0	5	1
871	0,0	5	1
835	0,0	5	1
Mean		5.3	1.3

