Localization of the "incline plane discrimination memory system" in the white rat

ROBERT THOMPSON, GREGORY J. ARABIE, and GREGORY B. SISK
Louisiana State University, Baton Rouge, Louisiana 70803

Blinded rats, previously trained to choose an upward sloping pathway and to avoid a downward sloping pathway (a vestibulo-kinesthetic discrimination problem), sustained bilateral cortical or subcortical lesions, and were subsequently tested for retention. Those animals earning zero or negative savings scores suffered damage to either the parietal cortex, cingulate cortex, corpus striatum, septofornix area, entopeduncular nucleus, posterolateral hypothalamus, anterior, ventromedial, lateral-ventral, or posterior thalamic nuclei, subthalamus, brainstem reticular formation, medial longitudinal fasciculus, red nucleus, ventral tegmental area, substantia nigra, interpedunculo-central tegmental area, or cerebellum. These results, coupled with earlier findings on the maze and visual discrimination habits, suggest that the incline plane habit is dependent upon the activities of three functional blocks of the brain: the first block (brainstem reticular formation and associated nuclei) has arousal and integrative functions, the second block (parietal cortex, cingulate cortex, septofornix area, thalamus, and cerebellum) has functions related to the construction and utilization of a nonvisual "cognitive map," and the third block (vestibular system) plays a role in spatial discrimination involving up vs. down.

As discussed earlier (Thompson & Thorne, 1973), the lesion method is ideally suited for the purpose of determining if a particular part of the brain is essential for the "memory" (expression) of a previously learned response. By canvassing many different brain areas with lesions (using, of course, different animals for different lesion placements), it is possible to map the "memory system" of the brain for any given learned response. Such a procedure has already been used to map the "visual discrimination" memory system (Thompson, 1969; 1976), the "manipulative response" memory system (Spiliotis & Thompson, 1973), and the "maze" memory system (Thompson, 1974) in the albino rat. The purpose of the current study was to map the "incline plane discrimination" memory system in this animal.

The incline plane problem usually consists of training the subject to choose a pathway that slopes upward and to avoid a pathway that either slopes downward (Lashley, 1929; Thompson, Malin & Hawkins, 1961) or is the horizontal position (Ghiselli & Brown, 1938; Ruch, 1927; 1930). In order to eliminate visual cues from controlling performance, the subject is either blinded or is run in the dark.

The sensory basis of this discrimination is not entirely known. Lashley (1929) and Ghiselli (1936) considered this problem to be a test of somesthetic (kinesthetic) sensitivity. Some support for this view was obtained when Ghiselli and Brown (1938) discovered that the acquisition of this habit is severely impaired following damage to either the medial lemniscus or the ventral thalamic nucleus. As pointed

out by Munn (1950), however, the possibility exists that vestibular cues might also play a role in the formation of this discrimination.

According to previous studies (Thompson, Malin, & Hawkins, 1961; Thompson, Duke, Malin, & Hawkins, 1961; Thompson & Hawkins, 1961; Thompson, Lukaszewska, Schweigerdt, & McNew, 1967; Thompson & Thorne, 1973), the retention of the incline plane problem is dependent upon the integrity of a number of brain structures, including the anterior one-half of the cerebral cortex, globus pallidus, anterior thalamus, posterior thalamus, lateral hypothalamic area, red nucleus, substantia nigra, region of the central gray, interpeduncular nucleus, and certain portions of the brainstem reticular formation. In the current experiment, virtually every part of the tel-, di-, mes-, and metencephalon was examined as to its contribution to the performance of the incline plane discrimination habit. In order to assess the role of vestibular cues, all brain-damaged subjects were checked for the expression of "labyrinthine righting reflexes."

METHOD

Subjects

Adult male albino rats ($n = 133$) of the Wistar strain were used. Prior to original learning, each subject was handled periodically, checked for middle-ear infection, and subsequently subjected to enucleation of the eyes and trimming of the vibrissae under deep chloral hydrate anesthesia.

Apparatus

A single-unit enclosed T-maze, adapted for the use of the motive of escape from footshock, was employed. The alleys, which measured 15.2 cm wide and 30.4 cm high, were covered

This research was supported in part by a grant from the Graduate Council on Research, Louisiana State University.

by a transparent Plexiglas sheet. The startbox was 30.4 cm long and the arms measured 45.6 cm long. At the end of each arm was a window through which the subject could enter an endbox. During training, a card was placed against each window. The startbox and arms of the T had a grid floor, whereas each endbox had a wooden floor. The entire T-maze was secured to a platform which could be tilted 11° laterally.

Procedure

During preliminary training, the apparatus was in the horizontal position. Each subject was trained to run from the startbox, through one of the arms, knock down the card, and enter the endbox in order to escape from (or avoid) footshock.

In original learning, each subject was trained to choose the arm that was inclined upward and to avoid the arm that was inclined downward. The position of the correct arm was varied from the right side to the left in a prearranged "random" order. The correct arm led to an endbox which was admissible by knocking down the unlocked card. The incorrect arm, however, led to a locked card which prevented the subject from entering the endbox on that side. Punishment for errors was given by charging the 7.5-cm grid section located below the locked card. The correction method was necessarily used. The specific training procedure was as follows: The subject was placed into the startbox and the startbox door was raised. Failure to leave the startbox within 5 sec was followed by brief footshocks. No further shock was given unless the subject made an error or unless the subject failed to traverse one of the arms within 15 sec. An error was defined as an approach response to the locked card which brought the subject's forefeet in contact with the charged grid section. Thus, the subject could enter the downward sloping arm without being charged with an error so long as the subject did not penetrate more than 38.1 cm. The subject was allowed to remain in the endbox for 10 sec, after which it was removed and placed into a restraining cage. Six trials were given daily with an intertrial interval of 60 sec. Training was terminated when the subject made a total of at least 11 correct responses within 2 consecutive days.

Following learning, 121 subjects were subjected to either cortical or subcortical lesions. Twelve subjects served as controls.

After a recovery (or rest) period of 10-20 days, all subjects were required to relearn the discrimination under the same conditions as those described in original learning. If the subject failed to reach the criterion of learning after making twice the number of errors required in original learning (earning an error savings score of -100%), the retention test was discontinued.

Swim Test

At the conclusion of postoperative training, each subject was given a "swim test" to check for the integrity of labyrinthine righting reflexes (see T'sang & Wu, 1936). The subject was suspended by its tail and placed into a sink (38.0 cm wide and 33.0 cm long) filled with water to a depth of 25.4 cm. If the subject floated and/or swam on top of the water (as normal rats usually do), a score of 1 was recorded. On the other hand, if the subject tucked its head downward while swimming on or beneath the surface (as rats with bilateral vestibular defects usually do), a score of 3 was recorded. A score of 2 was recorded when the subject dove toward the bottom without accompanying retroflexion of the head.

The swim test was repeated five times in succession. Repetition of the swim test was necessary because some subjects exhibited what appeared to be "learning"—they would swim beneath the surface during the first test, but would subsequently show a normal response on later tests. A mean score was computed for each subject.

Surgery and Histology

Bilateral lesions were customarily carried out in one stage under deep chloral hydrate anesthesia. For neocortical lesions and lesions

of certain other structures (cingulate cortex, ventral hippocampus, and cerebellum), the suction method was used. Subcortical lesions were made stereotaxically with reference to the rat atlas of Massopust (1961). Depending upon the area to be destroyed, a constant (anodal) current, ranging from 2 to 5 mA for a duration of 5-15 sec, was passed through an implanted stainless steel electrode with 1.0-2.0 mm of the tip exposed. In some cases, lesions were performed in two stages, with an interoperative period of 7-10 days.¹ Details of the surgical procedure have been reported earlier (Thompson, 1971).

At the conclusion of postoperative testing, each brain-damaged subject was sacrificed with an overdose of Nembutal, its vascular system perfused with normal saline followed by 10% Formalin, and the brain removed and stored in 10% Formalin for 2 days. For cortical injuries, the lesions were reconstructed on Lashley-type brain diagrams prior to sectioning. Each brain was sectioned frontally at 90 microns with the use of a freezing microtome. Every third section showing the lesion was photographed by using the section as a negative film on an enlarger (see Thompson, 1971). These photographs of unstained sections yield differentiation of the brain field similar to that obtained with a fiber stain, and readily permit identification of the central necrotic zone of the lesion (vacuolated area surrounded by a narrow rim of severely coagulated tissue) and the surrounding gliosis. Description of the lesions in the text will refer to the central necrotic zone only.

RESULTS

Original Learning

All subject succeeded in learning the incline plane discrimination problem within 14 days. Mean days and errors to criterion were 7.3 and 20.6, respectively.

Retention

Control Group

As shown in Table 1, retention of the problem (as measured by percentage error savings scores) was excellent: 7 of the 12 subjects in this group earned perfect savings scores.

The swim test revealed that of the combined 60 observations of the control subjects, a score above 1 was recorded on only two occasions.

Neocortex

Frontal area. Four subjects received bilateral lesions of the frontal cortex. The average extent of neocortical damage was 20.0% with a range of 14%-23%. Figure 1 shows the area of common bilateral damage sustained by these subjects. Three of the four subjects earned savings scores in excess of 79%.

The swim test was "negative" in all cases.

Parietal area. Four subjects sustained bilateral ablations of the parietal cortex, the amount of damage to the total neocortical surface ranging from 17% to 45% (mean = 31.2%). Figure 1 shows the area of common bilateral damage incurred in this group. All subjects earned savings scores below 38%.

In all cases, the swim test was negative.

Occipital area. A total of four subjects received bilateral lesions of the occipital cortex, the extent of damage ranging from 32% to 40% (mean = 35.2%). Figure 1 shows the area of common bilateral

Table 1
Mean Swim Test, Learning (Errors), and Retention (Percentage Error Savings) Scores for All Groups

Group	N	Swim Test Mean	Learning Mean	Retention	
				Mean	Range
Control	12	1.03	17.6	90.7	50 to 100
Neocortex					
Frontal	4	1.00	18.8	76.0	48 to 93
Parietal	4	1.00	16.2	-5.2*	-100 to 37
Occipital	4	1.00	21.4	87.4	75 to 100
Other Telencephalic Areas					
Limbic Cortex	2	1.00	34.0	-100.0*	
Amygdala	2	1.10	26.0	65.0	57 to 73
Septofornix Area	5	1.00	22.8	54.4*	-25 to 95
N. Accumbens Septi	2	1.00	21.0	31.0*	24 to 38
Dorsal Hippocampus	3	1.00	23.2	66.0	35 to 88
Ventral Hippocampus	3	1.00	17.3	76.7	75 to 78
Corpus Striatum	3	1.00	19.3	-4.7*	-100 to 53
Entopeduncular Nucleus	2	1.00	24.5	-7.5*	-50 to 35
Hypothalamus					
Anterolateral	2	1.00	24.5	86.0	72 to 100
Anteromedial	3	1.00	20.4	78.3	58 to 100
Posterolateral	4	2.60*	18.0	2.5*	-13 to 33
Posteromedial	3	1.73*	26.3	63.7*	60 to 71
Thalamus					
Anterior	2	1.00	17.0	-64.0*	-100 to -28
Dorsomedial	2	1.00	27.5	61.5	50 to 73
Ventromedial	3	1.13	21.3	-9.0*	-100 to 40
Lateral-Ventral	4	1.25	20.4	-32.5*	-100 to 8
Posterior	5	1.32	19.0	-11.3*	-50 to 23
Subthalamus	5	1.56	19.5	18.0*	-13 to 60
Brainstem Reticular Formation					
Anterior	4	2.20*	17.5	-72.5*	-100 to -46
Dorsal	3	2.13*	20.7	-15.7*	-100 to 63
Lateral	4	1.25	18.3	-17.5*	-100 to 52
Posterior	4	2.70*	19.5	-35.2*	-100 to 9
Other Brainstem Areas					
MLF	5	3.00*	26.5	-58.4*	-100 to 26
Medial Lemniscus	4	1.60*	20.5	78.2	61 to 100
Superior Colliculus	5	1.00	20.5	56.0*	11 to 93
Inferior Colliculus	2	1.00	30.5	100	
Red Nucleus	3	3.00*	17.0	-100.0*	
Ventral Tegmental Area	2	3.00*	25.0	-100.0*	
Substantia Nigra	6	1.00	23.5	16.5*	-20 to 48
Interpedunculo-Central Tegmental Area	3	3.00*	18.0	-42.2*	-100 to 33
Miscellaneous	5	1.00	19.0	80.4	58 to 100
Cerebellum	3	1.73	29.0	2.3*	-75 to 55

*Differed from the controls at least at the .05 level.²

damage sustained by these subjects. All achieved savings scores above 74%.

The swim test was negative throughout.

Summary. It would appear that the parietal cortex is more important for the expression of the incline plane problem than is either the frontal cortex or occipital cortex. In terms of savings scores, the parietal group was significantly inferior to both the occipital group and the frontal group ($p < .05$); the latter two groups did not differ significantly from each other.²

That lesion size alone was not responsible for this differential effect was shown by the insignificant

rank order correlation ($\rho = .05$) between the amount of neocortical damage and the extent of the retention loss for all 12 subjects.

Other Telencephalic Areas

Limbic cortex. Two subjects sustained bilateral ablations of the mesial cortex. In both cases, the lesions extended from the frontal poles to (or including) the retrosplenial cortex. The ablations extended approximately 2.0 mm laterally from the midline (damaging 7%-10% of the neocortical surface) and ventrally to the hippocampal surface. Neither subject was able to relearn the problem.³

Figure 1. Diagrams showing the region of common damage (stippled area) sustained by the frontal (F), parietal (P), and occipital (O) groups. The boundaries of Somatic Areas I and II were derived from Zubek (1951).

The swim test was negative in both cases.

Amygdaloid complex. The amygdaloid area was damaged bilaterally in two subjects. One suffered damage mainly to the corticomedial nuclear group, while the second sustained damage to both the corticomedial and basolateral nuclear groups (Figure 2A). The former earned a savings score of 73%, and the latter 57%.

Figure 2. Unstained sections derived from three rats showing lesions of the amygdala (A) and septal area (B, C). One rat with a septal lesion (B) earned a negative savings score, while the remaining two earned scores above 50%.

The swim test was negative in one case and only slightly positive in the second case.

Septofornix area. Five subjects sustained septal lesions which destroyed major portions of the medial and lateral nuclei. The descending fornix columns were interrupted in two cases. The subject with the ventralmost lesion (Figure 2B) earned a savings score of -25%. The remaining four earned scores between 61% and 95% (Figure 2C). As a group, these subjects were significantly inferior to the controls in retention of the incline plane discrimination.

The swim test was negative in all cases.

Nucleus accumbens septi. Two subjects sustained multiple lesions in the region of the nucleus accumbens septi. Portions of the lateral septal area and medial caudoputamen were also damaged (Figure 3A). Both subjects earned savings scores below 40%.

The swim test was negative in both cases.

Dorsal hippocampus. Three subjects received multiple electrolytic lesions of the dorsal hippocampus. While there was minimal damage to the overlying medullary substance, the dorsal thalamus was significantly invaded. Savings scores ranged from 35% (Figure 3B) to 88% (Figure 3C).

The swim test was negative in all cases.

Ventral hippocampus. Since posterior neocortical ablations failed to abolish the incline plane habit in the rat, it was decided to destroy the ventral hippocampus by aspiration through the overlying occipital cortex. Figure 4 shows the resulting ablation in one of three subjects. All earned savings scores in excess of 74%.

The swim test was negative throughout.

Corpus striatum. In two-stage operations, three subjects received multiple lesions of the ventral sector of the caudoputamen-pallidum complex. One failed to relearn the habit (Figure 5A), one earned a score of 33% (Figure 5B), and the remaining animal (with a somewhat asymmetrical lesion) earned a score of 53%.

The swim test was negative in all cases.

Figure 3. Unstained sections derived from three rats showing lesions of the nucleus accumbens septi (A) and the dorsal hippocampus (B, C). All three rats earned positive savings scores.

Entopeduncular nucleus. Two subjects sustained lesions in the region of the entopeduncular nucleus (Figure 5C). In contrast to the remaining animals of this experiment, these two subjects were seriously aphagic and adipsic throughout the entire post-operative period. Both, however, managed to relearn the problem with savings scores below 40%.

In both cases, the swim test was negative.

Hypothalamus

Anterolateral region. Two subjects sustained lesions of the medial forebrain bundle at preoptic (Figure 6A) or supraoptic levels. Both earned savings scores above 71%.

The swim test was negative in both cases.

Anteromedial region. Three subjects received lesions of the medial supraoptic hypothalamus. One achieved a savings score of 58% (Figure 6B), while the remaining two earned scores in excess of 75%.

The swim test was negative in all cases.

Posterolateral region. Four subjects received small bilateral lesions of the medial forebrain bundle at premamillary or mamillary levels (Figure 6C). All earned scores below 34%.

The swim test disclosed defective labyrinthine righting reflexes in all cases.

Posteromedial region. Three subjects were sub-

jected to lesions of the medial portions of the hypothalamus. Damaged structures included the ventromedial, dorsomedial, posterior, and mamillary nuclei (Figure 6D). All subjects earned savings scores between 60% and 71%.

The swim test disclosed a slight, but significant, defect in this group.

Thalamus

Anterior region. Two subjects received multiple electrolytic lesions which destroyed portions of the nucleus anterior ventralis, anterior medialis, anterior dorsalis, and medialis dorsalis. One rat failed to relearn the problem (Figure 7A), and the second earned a score of -28%.

The swim test was negative in both cases.

Dorsomedial region. Two subjects sustained medial thalamic lesions which destroyed most of the nucleus medialis dorsalis. One earned a savings score of 50%, and the second 73% (Figure 7B).

The swim test was negative in both cases.

Ventromedial region. Two subjects received small lesions localized at the base of the thalamus. Injured nuclei included the ventralis medialis, submedialis, rhomboideus, and medialis dorsalis (Figure 7C). These subjects earned savings scores of 33% and 40%. One additional subject, sustaining an extensive

Figure 4. Three unstained sections showing ablation of the ventral hippocampus and overlying neocortex in a rat earning a savings score of 77%.

Figure 5. Unstained sections derived from three rats showing lesions of the corpus striatum (A, B) and entopeduncular nucleus (C). One rat (B) earned a positive savings score, while the remaining two earned negative scores.

Figure 6. Unstained sections derived from four rats showing lesions of the hypothalamus. The rat with damage to the postero-lateral hypothalamus (C) earned a negative savings score, while the remaining three earned positive scores.

lesion to this area (Figure 7D), was unable to relearn the habit.

The swim test disclosed a slight defect in the subject with the largest lesion.

Lateral-ventral region. The four subjects of this group are of special importance because they sustained damage to thalamic regions (ventrobasal, lateral posterior, and ventrolateral complexes and the nucleus centralis lateralis) known to receive afferents from structures that may very well play a role in supporting the incline plane discrimination problem, namely, the cerebellum (Zeman & Innes, 1963), dorsal column nuclei (Lund & Webster, 1967a), spinal cord (Lund & Webster, 1967b), trigeminal nuclear complex (Lund & Webster, 1967b), and probably the vestibular nuclei (Deecke, Schwarz, & Fredrickson, 1974). Figure 8 shows the lesions of these four subjects. All performed poorly on the retention test.

The swim test disclosed a slight defect in the subject whose lesion is shown in Figure 8A.

Posterior region. Five subjects suffered caudal thalamic lesions. In two, the lesions destroyed portions of the medial lemniscus and the nucleus posterior thalami (Figure 9A). The remaining three had more medially placed lesions which damaged the nucleus parafascicularis and caudal portions of the medialis dorsalis. The habenulopeduncular tract was interrupted bilaterally in two cases (Figure 9B). All five subjects showed serious retention deficits.

The swim test disclosed a slight defect in the subject whose lesion is shown in Figure 9A.

Figure 7. Unstained sections derived from four rats showing lesions of the anterior (A), dorsomedial (B), and ventromedial (C, D) thalamic regions. Two (A, D) earned negative savings scores, while the remaining two earned positive scores.

Figure 8. Unstained sections derived from four rats showing lesions of the lateral-ventral thalamic complex. All earned savings scores below 10%.

Subthalamus

Four subjects suffered discrete lesions which destroyed the subthalamic nucleus bilaterally as well as portions of the underlying cerebral peduncle (Figure 9C). The savings scores ranged from -13% to 60%. One additional subject had a more medial lesion damaging Forel's fields H_1 and H_2 (Figure 9D); this subject earned a score of 0%.

The swim test revealed that three of the five subjects exhibited defective labyrinthine righting reflexes.

Figure 9. Unstained sections derived from four rats showing lesions of the posterior thalamus (A, B) and subthalamus (C, D). None earned a positive savings score.

cases, the caudal part of the substantia nigra suffered significant damage (Figure 10C). The three subjects with nigral involvement earned savings scores below 10%; the remaining subject earned a score of 52%.

Two of the four subjects showed imperfect labyrinthine righting reflexes.

Posterior region. Four subjects sustained bilateral damage to the paramedial portions of the reticular formation at rostral pontine levels. In all cases, the lesions destroyed the anterior portions of the

Brainstem Reticular Formation

Anterior region. Four subjects sustained lesions to the rostromedial extension of the reticular formation at the diencephalic juncture (Figure 10A). In no case did the lesions invade either the red nucleus or the habenulopeduncular tract, but there was significant encroachment on the posterior commissure and its associated nuclei, the central gray substance, and the nucleus parafascicularis. All subjects earned negative savings scores.

The swim test was positive in all cases.

Dorsal region. In two-stage operations, the reticular zone between the central gray and the red nucleus or postrubral area (which, in primates, is occupied by the central tegmental fasciculus) was damaged in three subjects. The central gray substance received significant damage, but the red nucleus was largely spared (Figure 10B). Two of the three subjects earned negative savings scores.

The swim test was positive in all subjects.

Lateral region. The reticular formation dorsal to the caudal extension of the substantia nigra was damaged to varying degrees in four subjects. In three

Figure 10. Unstained sections derived from four rats showing lesions of the rostral (A), dorsal (B), ventrolateral (C), and caudal (D) portions of the brainstem reticular formation. All earned negative savings scores.

Figure 11. Unstained sections derived from four rats showing lesions in or around the medial longitudinal fasciculus. All earned negative savings scores, except the rat with a lesion dorsal to the medial longitudinal fasciculus (D).

nucleus reticularis pontis oralis (Figure 10D). One subject failed to relearn, and the remaining three earned scores of -50% , 0% , and 9% .

The swim test was positive in all cases.

Other Brainstem Areas

Medial longitudinal fasciculus. This tract is known to carry impulses generated by vestibular stimulation (Brodal, 1974). In order to assess the role of vestibular

cues in the performance of the incline plane problem, an attempt was made to interrupt this tract with small lesions either at pontine or mesencephalic levels. Six subjects were involved, but only five suffered lesions clearly invading the medial longitudinal fasciculus (Figure 11A, B, C). All five subjects earned savings scores below 27% and all showed total abolition of labyrinthine righting reflexes.

The sixth subject (Figure 11D) suffered a lesion which was dorsal to the medial longitudinal fasciculus. This subject, whose data are not figured in Table 1, earned a savings score of 96% and showed a normal response when given the swim test.

Medial lemniscus. To evaluate the role of kinesthetic cues in the performance of the incline plane problem, an attempt was made to interrupt the medial lemniscus at rostral pontine levels. Four subjects sustaining varying amounts of damage to the medial lemniscus (Figure 12) exhibited moderate to excellent retention of the habit.

The swim test was slightly positive in all cases.

Superior colliculus. Five subjects received multiple electrolytic lesions to the region of the superior colliculus. In three cases, the underlying central gray substance was damaged, but the pretectum remained largely intact (Figure 13A). These three subjects earned scores of 11% , 21% , and 75% . The remaining two subjects had smaller lesions which did not penetrate to the central gray area; they earned scores of 80% and 93% .

The swim test was negative in all cases.

Inferior colliculus. Two subjects sustained extensive damage to the inferior colliculus (Figure 13B). Both

Figure 12. Unstained sections derived from four rats showing lesions in the vicinity of the medial lemniscus. All earned savings scores in excess of 60% .

Figure 13. Unstained sections derived from four rats showing lesions of the superior colliculus (A), inferior colliculus (B), red nucleus (C), and ventral tegmental area (D). The former two rats earned positive savings scores, while the latter two earned negative scores.

earned perfect savings scores, and both showed normal reactions on the swim test.

Red nucleus. In two-stage operations, three subjects received lesions in the region of the red nucleus (Figure 13C). All failed to relearn the problem, and all showed serious deficits of the labyrinthine righting reflexes.

Ventral tegmental area. This area was damaged in two subjects (Figure 13D). Both failed to relearn the habit and both showed marked losses on the swim test.

Substantia nigra. Six subjects sustained varying amounts of damage to the substantia nigra (Figure 14A). All achieved savings scores below 50%, and all exhibited normal responses on the swim test.

Interpedunculo-central tegmental area. Three subjects received small midline lesions at the base of the midbrain. In one, the lesion destroyed portions of the interpeduncular nucleus and the overlying central tegmentum (Figure 14B). The lesions in the remaining two subjects were largely confined to the central tegmentum, damaging portions of the dorsal and median raphe nuclei. All subjects earned savings scores below 40%.

The swim test was positive in all cases.

Miscellaneous. In this group, five subjects sustained lesions to the lateral parts of the brainstem. In two, the lesions were localized at rostral mesencephalic levels, damaging the tegmentum dorsal to the lateral nucleus of the substantia nigra and medial to the medial geniculate nucleus (Figure 14C). The remaining three suffered lesions at the mes-metencephalic juncture (Figure 14D). All attained scores in excess of 57%.

The swim test was negative in all cases.

Cerebellum

In three subjects, the cerebellum was extensively ablated. A segment of the paraflocculus remained intact in all subjects and the anterior one-fifth of the cerebellum escaped injury in one subject. The subject with the smallest lesion relearned the habit with a savings score of 55%. The remaining two earned scores of 27% and -75%.

The swim test disclosed that only one subject (one of the two subjects with virtually total cerebellar removal) exhibited normal labyrinthine righting reflexes.

Summary: The Incline Plane Discrimination Memory System

The various groups of brain-damaged subjects studied in the current experiment fall neatly into one of three categories. The first category would consist of those groups showing significantly poorer savings scores than the controls and *containing subjects earning zero or negative savings scores*. The groups falling into this category suffered damage to either the parietal cortex, cingulate cortex, septofornix

Figure 14. Unstained sections derived from four rats showing lesions of the substantia nigra (A), interpedunculo-central tegmental area (B), area of the medial geniculate nucleus (C), and the lateral brainstem (D). The former two earned negative savings scores, while the latter two earned positive scores.

area, corpus striatum, entopeduncular nucleus, posterolateral hypothalamus, anterior thalamus, ventromedial thalamus, lateral-ventral thalamus, posterior thalamus, subthalamus, brainstem reticular formation, medial longitudinal fasciculus, red nucleus, ventral tegmental area, substantia nigra, interpedunculo-central tegmental area, or cerebellum. The second category would consist of those groups showing significantly poorer savings scores than the controls, but devoid of any subjects earning zero or negative savings scores. The groups falling into this category sustained damage to either the nucleus accumbens septi, posteromedial hypothalamus, or superior colliculus. The third category would consist of those groups that earned savings scores which did not differ significantly from those earned by the controls. The groups falling into this category had damage to either the frontal cortex, occipital cortex, amygdala, hippocampus, anterolateral hypothalamus, anteromedial hypothalamus, dorsomedial thalamus, medial lemniscus, inferior colliculus, or lateral brainstem.

On the basis of the foregoing classification, those brain-damaged groups falling within the first category showed the most dramatic deficit in the memory (expression) of the incline plane problem. Mapping the critical areas for this deficit (the composite of which will be termed the "incline plane discrimination memory system") was based upon the distribution of lesions sustained by the subjects from these groups that earned zero or negative savings scores. Figures 15 and 16 depict these critical areas (cross-hatched areas on the left side of each diagram or

section). For comparative purposes, the critical areas making up the "visual discrimination memory system" (stippled areas on the right side of each diagram or section) are also presented. The latter areas were derived from an analysis of over 500 brain-damaged rats previously trained on brightness and/or pattern discrimination problems (see Thompson, 1976).

DISCUSSION

Sensory Basis of the Incline Plane Discrimination Habit

As mentioned at the outset of this paper, the incline plane problem has commonly been regarded to be a test of somesthetic (kinesthetic) sensitivity. The main support for this view has come from the findings that lesions of either the ventral thalamic nucleus or the medial lemniscus (at thalamic levels) retard acquisition of the incline plane habit (Ghiselli & Brown, 1938).

On the basis of more recent experimental findings, however, it is clear that the results of Ghiselli and Brown are not selectively supportive of the view that the incline plane problem involves the discrimination of kinesthetic cues. First of all, some evidence exists that cells within and around the ventrobasal thalamic group in the monkey respond to stimulation of the vestibular nerve (Deecke et al., 1974) and that these cells may constitute the thalamic relay in the vestibulo-cortical pathway (Fredrickson, Figge, Scheid, & Kornhuber, 1966). Second, lesions of the medial lemniscus at thalamic levels would undoubtedly invade the overlying ventral thalamus, the underlying subthalamus, or both. As shown in the current study, retention deficits on the incline plane habit were commonly observed in the presence of either ventral thalamic or subthalamic lesions alone.

According to the results of the current experiment, vestibular cues may play a greater role in the performance of the incline plane discrimination than kinesthetic cues. This conclusion is based upon the following observations: (a) Small lesions interrupting the medial longitudinal fasciculus at either mesencephalic or metencephalic levels produced dramatic deficits in retention of the incline plane habit; similarly placed lesions do not disrupt retention of visual discrimination habits (Thompson & Thorne, 1973), (b) of the 18 brain-damaged subjects exhibiting total loss of labyrinthine righting reflexes, as measured by the swim test (obtaining a mean score of 3.00), 9 failed to relearn the incline plane problem, 7 earned zero or negative savings, and only 2 earned positive savings (26% and 33%), and (c) those 4 subjects sustaining lesions of the medial lemniscus at rostral pontine levels earned savings scores on the incline plane problem which were not significantly inferior to those of the controls.

While the foregoing data give precedence to vestibular cues over kinesthetic cues in the execution of the incline plane problem, they are not of sufficient strength to warrant the conclusion that this task is a test of vestibular sensitivity. For example, it is not unreasonable to assume that kinesthetic signals mediated by direct spinothalamic pathways may play some role in the establishment of the discrimination habit. Furthermore, it is quite conceivable that lesions of vestibular pathways may disturb postural mechanisms (or disorganize central kinesthetic systems) to the degree that kinesthetic signals lose their differential character.

Perhaps the only position to take on this matter at the present time is to conceive of the incline plane problem as a bimodal sensory (kinesthetic and vestibular) discrimination task. From a neurophysiological point of view, this position is not unreasonable. As demonstrated by Schwarz and Fredrickson (1971) in the rhesus monkey, the "vestibulo-cortical" pathway, rather than being strictly modality specific, is activated by both vestibular and kinesthetic afferents. This would also make functional sense. As pointed out by Schwarz and Fredrickson (1971), overall perception of body position must require the combined (integrated) input of both vestibular (head position) and kinesthetic (joint position) impulses.

Incline Plane Discrimination Memory System vs Visual Discrimination Memory System

Probably the most relevant comparison to be made in connection with the data on the incline plane discrimination memory system (IPDMS) would be with those data on the visual discrimination memory system (VDMS). The problems from which these two memory systems were mapped are about of equal difficulty (Howze, 1974; Thompson & Craddock, 1972) and demand the same sort of response—approach one of two adjacent discriminanda. As shown in Figures 15 and 16, some remarkable similarities as well as differences occur in the composition of the respective memory systems.

Before dealing with this comparison, it is important to note that several methodological differences (aside from the sense modality involved) did exist between the study of the incline plane problem in the current experiment and the study of visual discrimination problems in previous experiments (see Thompson, 1976). While the experimental procedures overlapped at certain points (subjects of the same strain and of comparable age and previous experience, lesions of comparable size and location, motive of escape from footshock, displacement of a card in order to gain access to the goalbox, punishment of errors, correction allowed after the commission of an error, and an intertrial interval of 60 sec), they differed with respect to (a) number of trials

Figure 15. Schematic drawings of the dorsal and lateral surface of the cerebral cortex (upper panel) and a parasagittal section (lower panel) of the rat brain. Cross-hatched areas on the left side indicate composite lesion placements leading to zero or negative savings scores on the incline plane discrimination problem. Stippled areas on the right side indicate composite lesion placements leading to zero or negative savings scores on visual discrimination problems (see Thompson, 1976).

given daily (eight trials for the visual problems vs. six trials for the incline plane problem), (b) criterion of learning (15 correct responses within 2 consecutive days vs. 11 correct responses within 2 consecutive days), (c) treatment of subject after entering the goalbox (the subject was allowed to remain in the goalbox for the duration of the intertrial interval vs. the subject was removed from the goalbox after 10 sec and placed into a restraining cage for the remainder of the intertrial interval), and (d) apparatus (a rectangular-shaped choice chamber vs. a T-maze).

The extent to which any one (or any combination) of the foregoing methodological differences contributed to the differential make-up of the IPDMS as against the VDMS cannot be ascertained at the present time. In the succeeding discussion, however, it will be assumed that these methodological variations had virtually no influence on the outcome of local brain lesions in the albino rat and that all dissimilarities existing between the IPDMS and the VDMS arose from the difference in the sense modalities used to form the basis of the discriminative response.

Similarities

As shown in Figures 15 and 16, all of the similarities between the IPDMS and the VDMS occur at brainstem levels. In fact, there is a continuous overlap of critical areas extending from the pontine reticular formation (Figure 16L), through the midbrain (Figures 16H, 16I, 16J, 16K) and diencephalon (Figures 16D, 16E, 16F, 16G) to the corpus striatum (Figure 16A). This overlap includes such structures as the midbrain reticular formation, interpedunculo-central tegmental area⁴, red nucleus, substantia nigra, ventral tegmental area, posterior thalamus (principally the nucleus parafascicularis and posterior),

subthalamus, lateral hypothalamic area, entopeduncular nucleus, and probably the globus pallidus.

As pointed out earlier (Thompson, 1976), the foregoing ensemble of subcortical structures (whose morphological continuity conspicuously coincides with the ascending fiber systems associated with the brainstem reticular formation and the substantia nigra) has been termed the "general memory system" to the extent that discrete lesions placed anywhere within this ensemble disrupt the performance of a wide variety of previously learned habits in the rat. The functional significance of this ensemble remains obscure, but it is likely to be concerned with arousal and integrative activities.

Differences

Some very striking differences are present between the composition of the IPDMS and that of the VDMS. At the neocortical level, for example, the former includes the major portion of the parietal cortex, whereas the latter embraces mainly the occipital cortex (Figure 15, upper panel). There is little doubt that this difference is attributable to the different sense modalities involved in the performance of the two discrimination tasks.

Aside from the occipital cortex, only two other structures (three if the optic pathway to the lateral geniculate nuclei is included) appear to be included within the VDMS that are not represented within the IPDMS. These are the lateral geniculate nuclei (Figure 16F) and the lateral half of the cerebral peduncle at nigral levels (Figures 16H, 16I, 16J). As suggested elsewhere (Thompson, 1965; Thompson & Craddock, 1972), certain visual discrimination habits acquired by the rat may be mediated by a pathway that extends from the retino-geniculo-occipital complex to the nucleus cuneiformis of the

Figure 16. Twelve frontal sections through the brainstem based upon the Massopust (1961) stereotaxic atlas. Cross-hatched areas on the left side of each section indicate composite lesion placements leading to zero or negative savings scores on the incline plane discrimination problem. Stippled areas on the right side of each section indicate composite lesion placements leading to zero or negative savings scores on visual discrimination problems (see Thompson, 1976). Abbreviations: AT = anterior thalamus; CI = inferior colliculus; CG = central gray; CP = caudoputamen; DM = dorsomedial thalamus; EP = entopeduncular nucleus; FX = fornix column; GL = lateral geniculate nucleus; IP = interpeduncular nucleus; L = lateral thalamus; LH = lateral hypothalamic area; MB = mamillary bodies; ML = medial lemniscus; MRF = midbrain reticular formation; MT = mamillothalamic tract; NP = nucleus pontis; OC = optic chiasma; PRF = pontine reticular formation; RN = red nucleus; S = septal area; SC = superior colliculus; SN = substantia nigra; ST = subthalamic nucleus; V = ventral thalamus; VM = ventromedial thalamus.

mesencephalic reticular formation via the lateral half of the cerebral peduncle. Some recent support for this possibility may be found in studies by Howze (1974) and Petit and Thompson (1974).

Inspection of Figures 15 and 16 reveals that considerably more structures of the brain are included within the IPDMS than are represented within the VDMS. These additional structures include the cingulate cortex (Figure 15, lower panel), cerebellum (Figure 15, lower panel), septal area (Figure 16A), anterior thalamus (Figure 16B, 16C), lateral-ventral thalamic complex (Figures 16D, 16E), ventromedial thalamus (Figure 16D), and the area around and including the medial longitudinal fasciculus (Figures 16I, 16J, 16K, 16L). On the basis of this comparison, the performance of the incline plane discrimination problem requires the integrity of many more brain structures than is required for the per-

formance of visual discrimination problems. Furthermore, it would appear that *all of the foregoing structures that are peculiar to the IPDMS have sensory functions related to the vestibular and/or kinesthetic modalities*. Such a complex picture of the sensory discriminative mechanism underlying the performance of the incline plane problem raises doubt concerning the commonly held view that afferent impulses ascend to the thalamus, thence to the sensory cortical receiving areas, and from there to the motor cortex or some subcortical correspondent.

An Interpretation

On the strength of the preceding analysis, the IPDMS can be separated into a nonspecific division (consisting of those structures of the IPDMS that are also represented within the VDMS) and a specific division (consisting of those structures of the IPDMS that are not represented within the VDMS). As discussed earlier (Thompson, 1974, 1976), the nonspecific division may have arousal and integrative functions.⁵ The functions of the specific division of the IPDMS (SD-IPDMS), however, remain to be explicated.

One clue to the possible significance of such a complex sensory discriminative mechanism supporting the incline plane habit comes from the finding that every component of the SD-IPDMS, except one, is likewise essential for the performance of a maze habit (Thompson, 1974). (The exception is the area around and including the medial longitudinal fasciculus.) This striking degree of correspondence at the anatomical level suggests that the two habits have certain features in common with each other at the behavioral level. Clearly, one common feature is that the learned response, rather than being dependent upon and guided by visual cues (as is the learned response involved in visual discrimination habits), is dependent upon and guided by spatial cues (up vs. down or left vs. right). Guidance of these responses must necessarily be carried out by an ensemble of structures that not only processes spatial cues (and possibly response-produced cues), but very probably utilizes these cues to form an internal representation of the environment—a “cognitive map” (Tolman, 1948)—from which the subject can direct and monitor his movements in nonvisual space. This ensemble, we propose, embodies all of the components of the SD-IPDMS, except the area around and including the medial longitudinal fasciculus.

As noted above, the incline plane habit, in contrast to the maze habit, appears to be dependent upon the presence of vestibular cues. This finding suggests (but is by no means conclusive) that vestibular cues, while being essential for a spatial discrimination involving up vs. down, are not essential for a spatial discrimination involving left vs. right. On the other

hand, the maze habit, in contrast to the incline plane habit, requires the integrity of an additional block of structures; namely, the occipital cortex, hippocampus, and mamillary bodies (Thompson, 1974).⁶ This finding, in turn, suggests that the foregoing three structures are concerned with a spatial discrimination (or a series of spatial discriminations) involving left vs. right, but are not concerned with a spatial discrimination involving up vs. down.

Thus, the neural substrate underlying all spatial discriminations may involve a core of structures which contains at the very minimum the parietal cortex, cingulate cortex, septal area, anterior, ventromedial, lateral, and ventral thalamic nuclei, and the cerebellum. This core is conceived to participate (either directly or indirectly) in the construction of a cognitive map from which the subject can maneuver in space in the absence of visual cues. If the relevant spatial cues in a discrimination problem are related to up vs. down (e.g., incline plane habit), then the vestibular nuclei and its associated tracts must be coupled with this core in order to mediate the discriminative response. On the other hand, if the relevant spatial cues in a discrimination problem are related to left vs. right (e.g., maze habit), then the occipital cortex, hippocampus, and mamillary bodies must be coupled with this core in order to mediate the discriminative response.

Some support for these notions comes from a study recently completed at the Louisiana State University laboratory. Specifically, it was found that normal retention of a successive visual discrimination habit (go left in the presence of two black cards and go right in the presence of two white cards) requires the integrity of the retino-geniculo-occipital complex, hippocampus, and every component of the SD-IPDMS, except the area around and including the medial longitudinal fasciculus. It will be noted that this task involves not only a visual discrimination, but a spatial discrimination as well. It would be expected, therefore, that the memory system for the successive visual discrimination habit would embrace components of both the VDMS and the IPDMS. The inclusion of the hippocampus and the exclusion of the medial longitudinal fasciculus would follow from the fact that the successive habit requires a left-right discrimination rather than an up-down discrimination.

The neatness of the foregoing formulation, however, is not without complications. For example, in the recently completed study mentioned above, lesions of the mamillary bodies did not seriously impair retention of the successive visual discrimination habit. Since mamillary body damage does abolish a complex maze habit (Kaada, Rasmussen, & Kveim, 1961; Thompson, 1974), but does not abolish a successive visual discrimination habit, the possibility exists that the mamillary nuclei participate in spatial

discriminations only under circumstances in which a series (or temporal ordering) of left and right turns is required.

Finally, the question arises concerning the extent to which the SD-IPDMS participates in the performance of skilled movements. Clearly, such movements may be performed in the absence of visual cues. Unfortunately, little is known about the subcortical mechanisms underlying the execution of skilled movements and the one study that attempted to fill this hiatus (Spiliotis & Thompson, 1973) utilized a paucity of subjects within each group and examined only a few areas of the brain, mainly those structures composing the nonspecific division of the IPDMS.⁷ Further research is needed in order to answer this important question.

REFERENCES

- ALEXINSKY, T., & HOUCINE, O. CM-Pf thalamic complex and alimentary conditioning. *Brain Research*, 1973, **55**, 149-158.
- BRODAL, A. Anatomy of the vestibular nuclei and their connections. In H. H. Kornhuber (Ed.), *Handbook of sensory physiology. Vestibular system: Basic mechanisms*. New York: Springer-Verlag, 1974.
- DEECKE, L., SCHWARZ, D. W. F., & FREDRICKSON, J. M. Nucleus ventroposterior inferior (VPI) as the vestibular thalamic relay in the rhesus monkey. I. Field potential investigation. *Experimental Brain Research*, 1974, **20**, 88-100.
- DOMESICK, V. B. Projections from the cingulate cortex in the rat. *Brain Research*, 1969, **12**, 296-320.
- FREDRICKSON, J. M., FIGGE, U., SCHEID, P., & KORNUBER, H. H. Vestibular nerve projection to the cerebral cortex of the rhesus monkey. *Experimental Brain Research*, 1966, **2**, 318-327.
- GHISELLI, E. E. The effects of lesions in the spinal cord on the ability of the rat to discriminate differences in inclined planes. *Journal of Comparative Psychology*, 1936, **22**, 319-323.
- GHISELLI, E. E., & BROWN, C. W. Subcortical mechanisms in learning. V. Incline plane discrimination. *Journal of Comparative Psychology*, 1938, **26**, 271-285.
- HOWZE, M. A. The lateral cerebral peduncle: Its functional significance for the acquisition of visual and kinesthetic discriminations in the rat. *Physiological Psychology*, 1974, **2**, 500-508.
- KAADA, B. R., RASMUSSEN, E. W., & KVEIM, O. Effects of hippocampal lesions on maze learning and retention in rats. *Experimental Neurology*, 1961, **3**, 333-355.
- LASHLEY, K. S. *Brain mechanisms and intelligence*. Chicago: University of Chicago Press, 1929.
- LUND, R. D., & WEBSTER, K. E. Thalamic afferents from the dorsal column nuclei. *Journal of Comparative Neurology*, 1967, **130**, 301-312. (a)
- LUND, R. D., & WEBSTER, K. E. Thalamic afferents from the spinal cord and trigeminal nuclei. *Journal of Comparative Neurology*, 1967, **130**, 313-328. (b)
- MANN, H. B., & WHITNEY, D. R. On a test of whether one of two random variables is stochastically larger than the other. *Annals of Mathematical Statistics*, 1947, **18**, 50-60.
- MASSOPUST, L. C. Stereotaxic atlases: A. Diencephalon of the rat. In D. E. Sheer (Ed.), *Electrical stimulation of the brain*. Austin: University of Texas Press, 1961.
- MCNEW, B. R., & THOMPSON, R. Effect of posterior thalamic lesions on retention of a brightness discrimination motivated by thirst. *Journal of Comparative and Physiological Psychology*, 1966, **62**, 125-128.
- MUNN, N. L. *Handbook of psychological research on the rat*. Boston: Houghton Mifflin, 1950.

- PETIT, T. L., & THOMPSON, R. Nucleus cuneiformis lesions: Amnesic effects on visual pattern discrimination in the rat. *Physiological Psychology*, 1974, **2**, 126-132.
- RUCH, T. C. Preliminary study of the ability of the albino rat to discriminate inclined planes. *Journal of Comparative Psychology*, 1927, **7**, 405-423.
- RUCH, T. C. The discrimination ability of albino rats measured by a triple-unit incline plane discrimination apparatus. *Journal of Comparative Psychology*, 1930, **10**, 11-34.
- SCHWARZ, D. W. F., & FREDRICKSON, J. M. Rhesus monkey vestibular cortex: A bimodal primary projection field. *Science*, 1971, **172**, 280-281.
- SPILOTIS, P. H. *The effect of ventral midbrain lesions on retention of a brightness discrimination motivated by thirst in the rat*. Unpublished thesis, Louisiana State University, 1971.
- SPILOTIS, P. H., & THOMPSON, R. The "manipulative response memory system" in the white rat. *Physiological Psychology*, 1973, **1**, 101-114.
- THOMPSON, R. Centrencephalic theory and interhemispheric transfer of visual habits. *Psychological Review*, 1965, **72**, 385-398.
- THOMPSON, R. Localization of the "visual memory system" in the white rat. *Journal of Comparative and Physiological Psychology Monograph*, 1969, **69**, Part 2, 1-29.
- THOMPSON, R. Introducing subcortical lesions by electrolytic methods. In R. D. Myers (Ed.), *Methods in psychobiology*. New York: Academic Press, 1971.
- THOMPSON, R. Localization of the "maze memory system" in the white rat. *Physiological Psychology*, 1974, **2**, 1-17.
- THOMPSON, R. Stereotaxic mapping of brain stem areas critical for memory of visual discrimination habits in the rat. *Physiological Psychology*, 1976, **4**, 1-10.
- THOMPSON, R., & CRADDOCK, S. N. Lateral cerebral peduncle lesions: Amnesic effects on a visual habit in the rat. *Psychonomic Science*, 1972, **27**, 140-142.
- THOMPSON, R., DUKE, R. B., MALIN, C. F., & HAWKINS, W. F. The interpeduncular nucleus and retention in albino rats. *Journal of Comparative and Physiological Psychology*, 1961, **54**, 329-333.
- THOMPSON, R., & HAWKINS, W. F. Memory unaffected by mamillary body lesions in the rat. *Experimental Neurology*, 1961, **3**, 189-196.
- THOMPSON, R., LUKASZEWSKA, I., SCHWEIGERDT, A., & McNEW, J. J. Retention of visual and kinesthetic discriminations in rats following pretecto-diencephalic and ventral mesencephalic damage. *Journal of Comparative and Physiological Psychology*, 1967, **63**, 458-468.
- THOMPSON, R., MALIN, C. F., & HAWKINS, W. F. Effect of subcortical lesions on retention of a kinesthetic discrimination habit. *Experimental Neurology*, 1961, **3**, 367-374.
- THOMPSON, R., & THORNE, B. M. Brainstem reticular formation lesions: Amnesic effects on learned habits in the rat. *Physiological Psychology*, 1973, **1**, 61-70.
- TOLMAN, E. C. Cognitive maps in rats and men. *Psychological Review*, 1948, **55**, 189-208.
- T'SANG, Y., & WU, C. The effects of unilateral labyrinthectomy in the albino rat. *Chinese Journal of Physiology*, 1936, **10**, 571-598.
- ZEMAN, W., & INNES, J. R. M. *Craigie's neuroanatomy of the rat*. New York: Academic Press, 1963.
- ZUBEK, J. P. Studies in somesthesia. I. Role of the somesthetic cortex in roughness discrimination in the rat. *Journal of Comparative and Physiological Psychology*, 1951, **44**, 339-353.

NOTES

- Two-stage operations were routinely performed to damage the corpus striatum, red nucleus, and the dorsal portions of the midbrain reticular formation. This was done in order to reduce the severity and duration of aphagic-adipsic disturbances.
- The Mann-Whitney (1947) nonparametric (two-tailed) test was used throughout this paper.
- Since this paper was completed, we have obtained preliminary data on the comparison between anterior cingulate lesions ($N = 3$) and posterior cingulate lesions ($N = 3$) on retention of the incline plane problem. In accordance with the dichotomy suggested by Domesick (1969), the anterior group sustained extensive damage to the areas infradiata and precentralis agranularis, while the posterior group suffered virtually complete damage to both areas retrosplenialis granularis and agranularis. Although the anterior group tended to be more disturbed in relearning the habit than the posterior group (the difference in savings scores fell short of statistical significance), all subjects earned scores below the range generated by the control group.
- In the VDMS, the critical interpedunculo-central tegmental area resides .5 mm caudal to the section shown in Figure 16K (see Thompson, 1976). No data are available to determine if this region should also be included within the IPDMS.
- At this juncture, a question may arise concerning the extent to which the nonspecific division of the IPDMS (or VDMS) is a function of the use of escape from footshock as a motive. An intensive investigation of this problem has yet to be completed. However, the fact that lesions of either the corpus striatum (Spiliotis & Thompson, 1973), parafascicular-centre median complex (Alexinsky & Houcine, 1973), nucleus posterior thalami (McNew & Thompson, 1966), red nucleus (Spiliotis, 1971), interpedunculo-central tegmental area (Thompson et al., 1961), or the ventral portions of the brainstem reticular formation (Spiliotis & Thompson, 1973) significantly disturb habits based upon food or water reinforcements suggests that the nature of the motive underlying the performance of the learned response is not a critical variable.
- In the maze paper (Thompson, 1974), the septal area was not considered to be a component of the IPDMS, and therefore, was assumed to function in left-right discriminations, but not in up-down discriminations.
- In the Spiliotis and Thompson (1973) paper, it was claimed that all of the components of the SD-IPDMS function in the expression of skilled movements. While this may indeed be the case, empirical support for such a claim is lacking.

(Received for publication August 15, 1975;
revision accepted March 17, 1976.)