Brain mechanisms concerned with left-right differentiation in the white rat

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Rats previously trained on a successive brightness discrimination—go left in the presence of two black cards and go right in the presence of two white cards—sustained bilateral lesions to one of nine brain regions (parietal cortex, anterior cingulate cortex, posterior cingulate cortex, cerebellum, anterior thalamus, ventromedial thalamus, ventrolateral thalamus, lateral thalamus, and ventrobasal thalamus) thought to be concerned with the maintenance of habits having a proprioceptive-kinesthetic basis. The retention test disclosed that each of the nine brain-damaged groups showed significant deficits in the performance of the successive problem. Damage to the motor cortex, hippocampus, septofornix, or medial longitudinal fasciculus also led to significant retention deficits, but mammillary body or mediodorsal thalamic lesions had no effect. These findings suggest that left-right differentiation has a proprioceptive-kinesthetic basis in addition to a possible vestibular basis.

It has been proposed that the parietal cortex, cingulate cortex, cerebellum, and certain thalamic (anterior, lateral, ventrolateral, ventromedial, and ventrobasal) regions constitute a major part of the rat's somatosensory system concerned with the performance of learned habits having a proprioceptive-kinesthetic basis (Thompson, 1980, in press). The principle support for this hypothesis comes from the findings that those tasks most likely to have a proprioceptive-kinesthetic basis (simultaneous incline plane discrimination, maze habit, and latch box problems) are subject to interference by lesions to any one of the foregoing structures (Thompson, 1974; Thompson, Arabie, & Sisk, 1976; Thompson, Gates, & Gross, 1979), while those tasks least likely to have a proprioceptive-kinesthetic basis (simultaneous visual and odor discriminations) are not subject to interference by lesions to any one of the foregoing structures (Thompson, 1976, 1980).

While the sensory basis of telling left from right is far from being well established, it is not unreasonable to suppose that proprioceptive-kinesthetic signals play at least a supportive role in this differentiation. If this is indeed the case, then destruction of either the parietal or cingulate cortices, cerebellum, or certain thalamic regions rostral to the parafascicular nucleus should disrupt performance of a task dependent upon the differentiation between left and right.

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The task chosen for study was a "successive" brightness discrimination—go to the left window in the presence of two black cards and go to the right window in the presence of two white cards. After learning this task, different groups of rats sustained relatively discrete bilateral lesions to one of nine brain sites considered to be involved in the expression of habits having a proprioceptive-kinesthetic basis and were subsequently tested for retention. For comparative purposes, the effects of lesions to the frontal (motor) cortex, mediodorsal thalamic nucleus, dorsal hippocampus, septofornix area, mammillary bodies, and medial longitudinal fasciculus were also investigated.

It is important to emphasize that none of the brain regions examined in this experiment have been found to be critical for the performance of a simultaneous brightness discrimination habit—approach a white card and avoid an adjacent black card (Thompson, 1976)—and that the successive visual discrimination habit is considered to be an appropriate test of the ability of animals to differentiate left from right (Corballis & Beale, 1976).

METHOD

Subjects

Sixty-five adult male Wistar albino rats, weighing 400-650 g, were used. They were usually housed, two per cage, in medium-size wire cages containing a constant supply of food pellets and water. Prior to experimental training, each animal was handled periodically, checked for eye disease and middle ear infection, and subjected to trimming of the vibrissae.

Apparatus

A two-choice Thompson-Bryant discrimination box utilizing the motive of escape-avoidance of footshock was employed (see Thompson, 1978a). The startbox and choice chamber contained grid floors; the goalbox floor was made of wood. Two windows, 14.0 cm², located at the end of the choice chamber provided the only means by which the animal could enter the goalbox. During training, stimulus cards mounted on wooden blocks were placed against the windows.

The entire apparatus was painted flat black, except for the grid floor, vertically sliding Plexiglas startbox door, and Plexiglas lid. Illumination of the apparatus was provided by conventional ceiling fluorescent lights and a pair of fluorescent lamps (20 W each) placed 2.0 cm above the lid of the choice chamber. All parts of the grid floor were connected to an ac source regulated by a Variac.

Procedure

Original Learning

Following preliminary training, each rat was required to go to the right window when confronted with two white cards and to go to the left window when confronted with two black cards. An approach response to the unlocked correct card admitted the animal to the goalbox, whereas an approach response to the locked incorrect card was punished by mild footshock. The correction technique was used. The sequence in which the pairs of stimulus cards were presented followed a "prearranged" random order. Eight trials were given daily with an intertrial interval of 60 sec. The criterion of learning consisted of no more than one error in 2 consecutive days.

The specific training procedure was as follows: The rat was placed in the startbox, and the startbox door was raised. Failure to leave the startbox within 5 sec was followed by brief footshocks until the animal entered the choice chamber. No further footshocks were administered unless the animal made an error or failed to make a choice within 10 sec. An error was defined as an approach response to the incorrect card which brought the animal's forefeet in contact with the charged grid section located below the window.

Surgery

After learning the successive problem, the majority of animals sustained bilateral cortical or subcortical lesions. (Nine rats served as the normal control group.) All operations were carried out in one stage under deep chloral hydrate anesthesia. For cortical and cerebellar ablations, the suction method was used. Subcortical lesions were made stereotactically with reference to a modified version of the Massopust rat atlas (Thompson, 1978a). Depending upon the area to be destroyed, a constant anodal current of 2.0-3.0 mA for the duration of 10 sec was passed through an implanted stainless steel electrode with 1.0-2.0 mm of the tip exposed. Details of the surgical procedures have been reported elsewhere (Thompson, 1971).

Retention Test

Following a 14-day recovery (or rest) period, all animals were required to relearn the successive problem, the training procedure being the same as that described in original learning. Training was terminated when the animal reached the criterion of at least 15 correct responses within 2 successive days or when the animal made at least twice the number of errors required in original learning.

Retention was measured in terms of conventional error savings scores.

Histology

Upon completion of the postoperative test, each operated rat was killed with an overdose of chloral hydrate, its vascular system

was perfused with normal saline followed by 10% Formalin, and the brain was removed and stored in 10% Formalin for 2-4 days. For cortical injuries, the lesion was reconstructed on Lashley-type brain diagrams.

With a freezing microtome, each brain was sectioned frontally (sagittally in the case of the cerebellectomized preparations) at 90 microns. Every third section showing the lesion was then photographed at 12× by using the unstained section as a negative film in an enlarger (see Thompson, 1971).

RESULTS

Original Learning

All animals succeeded in learning the successive problem within 15 days. Mean days and errors to criterion were 6.7 and 21.9, respectively.

Retention

Control Group

As shown in Table 1, the control animals exhibited excellent retention of the successive problem. Three earned perfect savings scores, and only one earned a score below 85%.

"Proprioceptive-Kinesthetic" Groups

Parietal cortex. Figure 1 shows the cortical destruction suffered by the four animals in this group. In all cases, major portions of the primary somatosensory areas, as defined neurophysiologically by Hall and Lindholm (1974), were destroyed. Although the occipital cortex was spared, encroachment on the motor areas was evident in each case.

Although the lesions of these four animals did not differ appreciably in terms of locus or extent, savings scores ranged from -100% to 72%.

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

Group	N	Learning			Retention	
		Mean	Mean	Mean	Range	
Control	9	20.9	90.9		70-100	
Parietal Cortex	4	22.5	10.0*		-100-72	
Anterior Cingulate Cortex	4	32.2	-12.7*		-100-49	
Posterior Cingulate Cortex	4	26.5	34.5		-39-94	
Cerebellum	3	20.3	-22.3*		-100-33	
Anterior Thalamus	4	20.0	21.0*		-12-50	
Ventrolateral Thalamus	4	19.0	60.1*		50-84	
Ventromedial Thalamus	4	25.5	20.5*		-10-60	
Lateral Thalamus	4	19.0	-19.8*		-100-30	
Ventrobasal Thalamus	4	26.0	56.5*		20-91	
Frontal Cortex	3	25.3	76.0*		70-82	
Dorsal Hippocampus	4	20.5	50.0*		33-81	
Septofornix	3	26.0	54.7*		36-74	
Mammillary Bodies	4	21.5	85.0		77-95	
Mediodorsal Thalamus	3	21.0	75.3		40-94	
Medial Longitudinal Fasciculus	3	34.0	75.0*		72-78	

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

Figure 1. Reconstruction of cortical lesions (black areas) in four rats composing the parietal group. Numbers on the left and right sides of each diagram refer to estimated percentage damage to the neocortical surface and percentage error savings scores, respectively.

Anterior cingulate cortex. In two rats, the anterior division of the cingulate cortex (areas infraradiata and precentralis agranularis) was ablated. Two additional rats suffered damage to both the anterior and posterior divisions of the cingulate cortex (Figure 2, left column).

Figure 2. Reconstruction of cortical lesions (black areas) in those rats composing the anterior cingulate (left column) and posterior cingulate (right column) groups. (See Figure 1 for description of the numbers.)

Figure 3. Reconstruction of cerebellar lesions (cross-hatched areas) in three rats. Error savings scores were 33% (A), -100% (B), and 0% (C).

All animals earned savings scores below 50%.

Posterior cingulate cortex. Four rats received posterior cingulate (areas retrosplenialis granularis and agranularis) ablations that extended ventrally to the hippocampal surface (Figure 2, right column).

Because of the high savings score earned by one operated animal, the Mann-Whitney test failed to disclose a significant difference in retention scores between this operated group and the controls. However, three of the four posterior cingulate rats achieved scores below 51%, while all nine control rats achieved scores above 51%—this difference in proportions was found to be significant at the .05 level according to the Fisher exact probability (two-tailed) test.

Cerebellum. All three cerebellectomized rats (Figure 3) showed moderate to serious deficits in retention of the successive problem.

Anterior thalamus. Four animals sustained varying degrees of damage to the anterodorsal, anteroventral,

anteromedial, medioventral, paratenial, mediodorsal, and/or reticular nuclei (Figures 4A and 4B). The internal capsule was largely spared, but the stria medullaris received unilateral damage in two cases.

All four animals achieved savings scores below 51%.

Ventrolateral thalamus. The ventrolateral nucleus and portions of the lateral, centrolateral, and ventromedial nuclei were damaged in four rats (Figure 4C). Although not exhibiting serious relearning disturbances, these animals nevertheless earned savings scores that were significantly inferior to those earned by the controls.

Ventromedial thalamus. In four rats, the ventromedial thalamic nucleus was severely damaged (Figure 5A). In most cases, the lesions also invaded the mediodorsal, ventrolateral, medioventral, submedial, and central thalamic nuclei.

Figure 4. Photographs of unstained sections derived from three rats showing lesions to the anterior (A and B) and ventrolateral (C) thalamus. Savings scores were -12% (A), 11% (B), and 50% (C).

Figure 5. Photographs of unstained sections derived from three rats showing lesions to the ventromedial (A), lateral (B), and ventrobasal (C) thalamus. Savings scores were -10% (A), -15% (B), and 48% (C).

All animals of this group earned savings scores that were below the range established by the controls.

Lateral thalamus. The lateral dorsal and/or lateral posterior thalamic nuclei were damaged in four rats (Figure 5B). Other injured thalamic structures included the ventrolateral, centrolateral, ventrobasal, and posterior nuclei.

All animals exhibited poor retention of the successive problem.

Ventrobasal thalamus. Four rats received lesions to the ventrobasal thalamic complex which extended into the suprajacent lateral thalamic nuclei (Figure 5C). Savings scores disclosed a slight, but significant, deficit in retention of the successive habit.

Other Groups

Frontal cortex. All three rats with relatively discrete frontal (motor) cortical ablations (Figure 6)

earned savings scores within the range established by the control group.

Dorsal hippocampus. The four animals having multiple electrolytic lesions within the dorsal hippocampus (Figure 7A) showed only a slight retention loss on the successive problem.

Septofornix area. Two of the three animals with extensive damage to the septofornix area (Figure 7B) earned savings scores below the range of the control group.

Mammillary bodies. All four animals suffering lesions to the mammillary bodies (Figure 7C) showed good retention of the successive problem.

Dorsomedial thalamus. Two animals with relatively discrete lesions of the mediodorsal thalamic nucleus (Figure 8A) earned savings scores in excess of 90%. The third, which had a more ventrally placed lesion (damaging the central, medioventral, and submedial nuclei in addition to the mediodorsal nucleus), earned a score of 40%.

Figure 6. Reconstruction of cortical lesions (black areas) in three rats composing the frontal group. (See Figure 1 for description of the numbers.)

Figure 7. Photographs of unstained sections derived from three rats showing lesions to the dorsal hippocampus (A), septofornix (B), and mammillary bodies (C). Savings scores were 36% (A), 36% (B), and 95% (C).

It is interesting to note the lesion in one animal that damaged the more lateral portions of the medio-dorsal thalamic nucleus along with the centrolateral and lateral posterior nuclei (Figure 8B). This rat was unable to relearn the successive problem. (The data of this animal were not figured in Table 1.)

Medial longitudinal fasciculus. This tract, which is known to carry impulses generated by vestibular stimulation (Brodal, 1974), was interrupted at mesencephalic levels by small electrolytic lesions in three rats (Figure 8C). All animals earned savings scores within the range established by the control group.

Summary

Of the 15 brain-damaged groups investigated in this study, 13 earned savings scores that were significantly inferior to those earned by the control group. This pattern of results suggests that the successive visual discrimination habit is highly susceptible

to interference by brain damage. It is possible, however, to define a limited number of brain regions that appear to be more important for the maintenance of the successive habit than other regions. This was accomplished by charting the distribution of lesion placements in those animals earning zero or negative savings scores on the successive problem. The resulting map of critical areas is shown in Figures 9 and 10. Again, it should be emphasized that these critical areas have not been found to participate in the performance of simultaneous visual discrimination habits (see Thompson, 1976).

DISCUSSION

General Findings

Cortical Lesions

While each of the groups with frontal, parietal,

Figure 8. Photographs of unstained sections derived from three rats showing lesions to the dorsomedial thalamus (A), dorsomedial and lateral thalamus (B), and medial longitudinal fasciculus (C). Savings scores were 92% (A), -100% (B), and 75% (C).

anterior cingulate, or posterior cingulate ablations displayed a significant reduction in retention of the successive habit, it is important to note that the extent of the retention deficits was not related to the amount of damage to neocortical tissue alone. Considering the performance of all 15 cortically damaged rats studied in this experiment, the rank-order correlation between the extent of the retention deficit and the estimated amount of neocortical involvement was found to be $-.06$. Within-group comparisons also failed to disclose any trend indicative of a "mass action" effect (see Figures 1, 2, and 6).

Due to the relatively large cortical ablations, the small number of subjects within each group, and the intragroup uniformity of lesion placements, the data of the present study are inadequate either to delineate discrete cortical foci critical for successive discrimination deficits (beyond those shown in Figure 9) or to assess the relative contributions of each cortical region to the performance of the successive problem. However, comparisons of both mean savings scores and percentages of cases earning scores below the range established by the control group suggest that the anterior cingulate cortex is the most critical, while the frontal (motor) cortex is the least critical, for normal retention of the successive brightness discrimination habit—no overlap in savings scores occurred between these two groups. It is interesting to note that the same pattern of results appears to hold

Figure 9. Schematic drawings of the dorsal surface (A) and a parasagittal section (B) of the rat brain showing composite lesion placements (large black dots) leading to zero or negative error savings scores on the successive brightness discrimination problem. (Lesion placements are represented on only one side of the brain.)

Figure 10. Four frontal sections at successive levels through the thalamus showing composite lesion placements (large black dots) leading to zero or negative error savings scores on the successive brightness discrimination problem. (Lesion placements are represented on only one side of the brain.) Abbreviations: AD = anterodorsal nucleus, AM = anteromedial nucleus, AV = anteroventral nucleus, Ce = central medial nucleus, Cl = central lateral nucleus, LD = lateral dorsal nucleus, LP = lateral posterior nucleus, MD = mediodorsal nucleus, MV = medioventral nucleus, Pa = paratenial nucleus, R = reticular nucleus, Sm = submedial nucleus, VB = ventrobasal complex, VM = ventromedial nucleus, VL = ventrolateral nucleus.

for the incline plane discrimination problem (Thompson et al., 1976), a conventional 3-cul maze habit (Thompson, 1974), and a simple latch-box (button rotation) task (Thompson et al., 1979).

It should be pointed out that posterior cortical (occipital) ablations are apt to produce more serious relearning impairments on successive brightness discrimination habits than are any other cortical ablations (Bauer & Cooper, 1964; Isaacson, Schmaltz, & Douglas, 1966; Thompson & Malin, 1961). The role of the occipital cortex in the performance of the successive habit, however, is undoubtedly different (being related to visual capacities) from that of other cortical regions, since destruction of the former, but not of the latter, abolishes simultaneous brightness discrimination habits (Horel, Bettinger, Royce, & Meyer, 1966; Lashley, 1929; Thompson, 1976).

Cerebellar Lesions

Despite the presence of severe locomotor ataxia, cerebellectomized rats run reasonably well on aver-

sively motivated laboratory tasks (Thompson, 1969, 1974). In the present study, the three cerebellectomized rats earned savings scores of 33%, 0%, and -100%. That this retention loss is not entirely due to locomotor ataxia is suggested by the findings that similarly placed lesions do not seriously impair retention of simultaneous brightness (Thompson, 1969, 1976) or odor (Thompson, 1980a) discrimination tasks.

Subcortical Lesions

A significant impairment in retention of the successive habit was associated with lesions to any one of the thalamic nuclei investigated in this experiment, except the mediodorsal nucleus. Again, the paucity of subjects within each group combined with the investigation of relatively large thalamic lesions preclude any accurate delineation of critical thalamic foci for successive discrimination deficits or any reasonable assessment of the relative contributions of each thalamic region to the performance of the successive problem. Based on the analysis shown in Figure 10, however, it would appear that the anterior (particularly the anterodorsal and anteroventral), lateral, and ventromedial thalamic nuclei are more important for the survival of the successive habit than are the ventrobasal and ventrolateral thalamic nuclei.

In light of the findings of Isaacson et al. (1966) and Kimble (1963), it was expected that the successive problem would be seriously compromised by hippocampal lesions. This expectation was confirmed only to the extent that our hippocampal group was significantly inferior to the controls in retention scores. All four hippocampal-damaged rats, however, earned savings scores (33%, 36%, 50%, and 81%) reflecting some sparing of the successive habit. Conceivably, the dramatic retention deficits noted by Isaacson et al. may have arisen from extensive hippocampal damage, combined destruction of hippocampal and neocortical (occipital) tissue, or both, since their surgical procedure consisted of aspiration of neocortical tissue overlying the hippocampus followed by aspiration of the exposed hippocampus. An experiment involving the destruction of the major portion of the hippocampus by electrolytic means would be necessary to determine which of the foregoing alternatives accounts for the discrepancy between our results and those of Isaacson et al.

Although our hippocampal lesions were smaller than those investigated by Isaacson et al., comparable electrolytic lesions of the hippocampus have been reported to elicit severe relearning deficits on 3-cul maze habits (Thompson, 1974, 1979). This finding suggests, at the very least, that the hippocampus has greater functional significance for the performance of a maze habit than for the performance of a successive brightness discrimination habit. Consistent with this suggestion is the finding that lesions to

those structures anatomically related to the hippocampal formation (septofofnix area and mammillary bodies) produce either slight or no deleterious effects on the successive habit (present study), but virtually abolish a maze habit (Thompson, 1974).

Finally, lesions of the medial longitudinal fasciculus had only a small deleterious effect on retention of the successive problem. The significance of this finding relates to the fact that vestibular cues have been viewed by some investigators to be essential for spatial perception (Douglas, 1966; Douglas, Clark, Erway, Hubbard, & Wright, 1979), a topic that will be discussed later in this paper.

Successive Problem vs. Simultaneous Problem

The findings of the present study confirm earlier results (Kimble, 1963; Thompson, Baumeister, & Rich, 1962; Thompson & Malin, 1961) in showing that the neurological mechanism mediating a successive visual discrimination is not the same as that mediating a simultaneous visual discrimination. While the successive problem is subject to interference by lesions of the parietal cortex, cingulate cortex, cerebellum, hippocamposeptal complex, or certain thalamic nuclei rostral to the parafascicular nucleus (see Figures 9 and 10), the simultaneous problem is not (Thompson, 1969, 1976).

The role of this ensemble of structures in the performance of the successive problem is most likely associated with the involvement of spatial cues (Nissen, 1950; Spence, 1952). The subject must learn a left-going response to one stimulus configuration (two black cards) and a right-going response to a different stimulus configuration (two white cards). This is to be contrasted with the simultaneous problem in which the subject learns simply to approach the positive (white) card and/or avoid the negative (black) card (Nissen, 1950).

Based on the foregoing considerations, it seems reasonable to assume that those structures selectively involved in the successive visual discrimination habit have some function related to the differentiation between left and right.

Sensory Basis of Left-Right Differentiation

As shown in Figures 9 and 10, those areas critical for retention of the successive problem include the parietal cortex, cingulate cortex, cerebellum, and a conglomerate of thalamic nuclei. Since this block of structures has previously been found to be critical for retention of tasks likely to have a proprioceptive-kinesthetic basis, such as an incline plane discrimination (Thompson et al., 1976), a maze habit (Thompson, 1974, 1979), and latch-box tasks (Thompson et al., 1979), the possibility must be considered that left-right differentiation also has a proprioceptive-

kinesthetic basis or at least is dependent upon the activities of those central brain regions processing proprioceptive-kinesthetic signals.

In the investigation of spontaneous alternation behaviors, Douglas and his collaborators (Douglas, 1966; Douglas et al., 1979) have presented evidence that the spatial position sense may depend upon the vestibular system. Potegal, Day, and Abraham (1977), however, have reported data suggesting that proprioceptive-kinesthetic sensitivity as well as vestibular sensitivity may lie at the basis of spontaneous alternation.²

The notion that vestibular impulses might contribute to left-right differentiation was at least partially evaluated in the present experiment by examining the effects of lesions to the medial longitudinal fasciculus on retention of the successive habit. (Such lesions abolish retention of an up-down discrimination in rats—Thompson et al., 1976.) Although the three animals with lesions to this vestibular pathway exhibited typical loss of labyrinthine righting reflexes (retroflexion of head when suspended by the tail and swimming to the bottom of a tank of water), they showed no serious disturbance on the successive habit, earning savings scores within the range of the controls. These findings, of course, by no means prove that the vestibular system is not fundamental to the differentiation between left and right; after all, the medial longitudinal fasciculus is only one of several ascending pathways of the vestibular system (Brodal, 1974).

Until further data are available to evaluate this issue, it might be prudent to take the moderate position that left-right differentiation is a multimodal (proprioceptive-kinesthetic and vestibular) discrimination task. In support of this position is the finding that the "vestibulocortical" pathway in the rhesus monkey is activated by both vestibular and kinesthetic afferents (Schwarz & Fredrickson, 1971).

The "Proprioceptive-Kinesthetic Discriminative System"

On the whole, the results of the present investigation support the notion presented at the outset of this paper that those tasks likely to have a proprioceptive-kinesthetic basis (including the successive brightness discrimination) are susceptible to interference by lesions to the parietal cortex, cingulate cortex, cerebellum, or certain thalamic (anterior, lateral, ventrolateral, ventromedial, and ventrobasal) regions. While the frontal (motor) cortex, hippocampus, septofornix area, mammillary bodies, and medial longitudinal fasciculus participate in the maintenance of some habits having a proprioceptive-kinesthetic basis, they are not critical for others. For example, the hippocampus, septofornix, and mammillary bodies are not

essential for the performance of incline-plane (Thompson et al., 1976) or latch-box (Spiliotis & Thompson, 1973) tasks. Similarly, the frontal cortex is not involved in the performance of incline-plane (Thompson et al., 1976) or maze (Thompson, 1979) tasks, while the medial longitudinal fasciculus is not necessary for the survival of maze (Thompson, 1974) or latch-box (unpublished observations) habits.

If the parietal and cingulate cortices, cerebellum, and the above-mentioned thalamic nuclei do, indeed, form the core of a proprioceptive-kinesthetic discriminative system,³ then it may be necessary to reconsider Konorski's (1967) and Mowrer's (1960) notions that avoidance (both active and passive) habits have a proprioceptive-kinesthetic basis. According to one study (Thompson, 1978b), avoidance habits tend to be disorganized by selective lesions to many (but not all) components of the proprioceptive-kinesthetic discriminative system. It remains to be seen if other habits proposed to have a proprioceptive-kinesthetic basis, such as distance discrimination (Lukaszewska, 1973), time discrimination (Rosenkilde & Lawicka, 1977), and delayed-response learning (Manning, 1978), would also be subject to interference by discrete lesions to most components of this system.

Anatomical Considerations

Of all the structures making up the proposed proprioceptive-kinesthetic discriminative system, only the cerebellum, parietal cortex, and ventrobasal thalamus have traditionally been emphasized as major sites processing proprioceptive-kinesthetic signals (Zeaman & Innes, 1963). That the ventromedial and ventrolateral thalamic nuclei may also be involved in the sense of movement is suggested by the fact that these thalamic sites receive cerebellofugal fibers (Faull & Carman, 1978) and project, at least in part, to the parietal cortex (Donoghue, Kerman, & Ebner, 1979; Herkenham, 1979). Since the lateral thalamic complex receives a contingent of spinothalamic tract (Giesler, Menetrey, & Basbaum, 1979; Lund & Webster, 1967b) and medial lemniscus (Lund & Webster, 1967a) projections, it too may serve importantly in the perception of movement-produced stimuli (see Giesler et al., 1979). The posterior cingulate and anterior cingulate (prefrontal) regions of the rat brain would conceivably participate in proprioceptive-kinesthetic functions by virtue of their inputs from the ventromedial and lateral thalamic nuclei (Herkenham, 1979; Jones & Leavitt, 1974).

The extent to which the anterior thalamus plays a role in the discrimination of proprioceptive-kinesthetic signals remains to be determined. It apparently does not receive direct afferents from lemniscal or spinothalamic tracts, nor is it the target of cerebellofugal

fibers. Destruction of extraneous fiber systems coursing through the anterior thalamus (originating, for example, within the ventromedial and/or ventrolateral thalamic nuclei) could account for the retention losses associated with damage to the rostral portion of the thalamus.

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NOTES

1. The statistical evaluations were based on the Mann-Whitney (1947) nonparametric (two-tailed) test.

2. These findings on spontaneous alternation may be of limited relevance to the issue concerning the sensory basis of left-right differentiation since spontaneous alternation is tested only within the context of short-term memory. Left-right differentiation underlying the performance of a successive problem, in contrast, is tested within the context of long-term memory. Conceivably, vestibular sensitivity may provide a salient cue in short-term memory, but not in long-term memory, of spatial responses.

3. By virtue of its significance in motor control, the basal ganglia might be expected to play some role in the proprioceptive-kinesthetic discriminative process. However, the basal ganglia are excluded from the proprioceptive-kinesthetic discriminative system, because discrete lesions to this complex are apt to produce losses in retention of visual as well as nonvisual habits in the rat (Thompson, 1978a).

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ERRATUM

Moore, J. W., & Stickney, K. J. Formation of attentional-associative networks in real time: Role of the hippocampus and implications for conditioning, *Physiological Psychology*, 1980, 8, 207-217—This paper contains errors on two pages. On page 208, right-hand column, lines 3 and 4: The inequality signs are pointing in the wrong direction. On page 215, left-hand column, second line from bottom of page: V_X^A should be V_A^X .