Subcortical lesions and retention of a brightness discrimination in the rat: Appetitive vs. aversive motivation

ROBERT THOMPSON

*Fairview State Hospital, Costa Mesa, California 92626
and University of California Irvine Medical Center, Orange, California 92668*

and

PETER H. SPILIOTIS

Louisiana State University, Baton Rouge, Louisiana 70803

Thirsty rats, previously trained to approach a white card and avoid an adjacent black card to obtain water, sustained discrete bilateral lesions to certain brainstem sites and were subsequently tested for retention. Those lesion placements producing retention deficits on this appetitively motivated visual discrimination problem closely corresponded with those producing retention deficits on aversively motivated visual discrimination problems.

In an earlier paper (Thompson, 1976), a detailed description of those subcortical regions critical for retention of visual discrimination habits was given in the form of a stereotaxic map. The data from which this map was constructed were derived from over 500 brain-damaged rats that had preoperatively been trained on a brightness and/or a pattern discrimination task under the motive of escape-avoidance of footshock.

During the course of the foregoing investigation, we periodically examined the effects of lesions to certain subcortical sites on retention of a brightness discrimination habit learned under thirst motivation. This was done in order to determine whether the use of an appetitive motive would alter the character of the stereotaxic map of critical "visual discrimination" structures achieved with the use of an aversive motive. However, rather than surveying virtually the entire neuraxis with discrete lesions, as was done in the earlier paper, we concentrated only on those sites found to be essential for normal retention of aversively motivated visual discrimination habits.

In the current paper, a summary of the retention data on an appetitively motivated white-black discrimination is given and compared with that on aversively motivated visual discriminations.

MATERIALS AND METHODS

Adult male albino rats of the Wistar strain were used. They were placed on a 23.5-h watering schedule 5 days prior to preliminary training. With the use of a modified two-choice Thompson-Bryant (1955) discrimination box, these animals were initially trained to run from the startbox through the choice chamber, displace a medium gray card blocking the window, and enter a

gray compartment in order to obtain water. Subsequently, the animals were trained on the white-black discrimination problem. An approach response to the white card led to a white compartment containing a dish of water from which the animal could drink for 5-10 sec. On the other hand, an approach response to the black card led to a black compartment containing no water. A error was defined as the rat's making contact with the black card, whether or not it fully entered the black compartment. (The correction method was used throughout.) The position of the cards was switched from the right to the left window in a prearranged "random" order. Six trials were given daily with an intertrial interval of 5 min. The criterion of learning was met when the rat made no more than one error in 2 consecutive days.

Following learning (or, in some cases, overlearning), most of the animals were subjected to one-stage bilateral subcortical (electrolytic) lesions under deep chloral hydrate anesthesia. Two-stage lesions (a unilateral lesion followed by a contralateral lesion with an interoperative period of 7-10 days), however, were usually made in those animals designated to receive destruction of the globus pallidus, red nucleus, ventral tegmental area, or midbrain reticular formation. An attempt was made to produce lesions comparable in both locus and size to those sustained by rats in earlier studies that showed retention losses on aversively motivated visual discrimination tasks (Thompson, 1978).

Following a recovery period (or rest period in the case of the normal controls) of 2-3 weeks, all rats were given a retention test involving relearning of the white-black discrimination. The relearning procedure was the same as that described in original learning. If an animal failed to reach the criterion after committing at least twice the number of errors required in original learning, the retention test was terminated at that point. Conventional percentage error savings scores constituted the measure of retention, the poorest savings score being - 100%.

At the conclusion of the retention test, each brain-damaged rat was killed with an overdose of chloral hydrate. Its vascular system was then perfused with normal saline followed by 10% Formalin, the brain was removed and stored in 10% Formalin for 2-5 days. With a freezing microtome, each brain was sectioned frontally at 90 μ . Every third section showing the lesion was subsequently photographed at 10-14 $\times$ by using the section as a negative film in an enlarger.

Table 1
Mean Savings Scores for All Groups and Percentage of Rats From Each Group Earning Zero or Negative Savings (P)

Group	N	Mean Savings	Range	P
Control	24	91.0	70-100	.0
Globus Pallidus	4	22.5	- 10- 60	25.0
Entopeduncular Nucleus	3	16.7	- 8- 58	66.7
Lateral Hypothalamus	3	.0	- 40- 50	66.7
Subthalamus	3	- 11.0	- 88- 41	33.3
Nucleus Posterior Thalami	8	3.6	-100- 79	25.0
Nucleus Parafascicularis	4	- 16.7	-100- 42	50.0
Pretecal Area	2	25.0	- 8- 58	50.0
Prerubral Reticular Formation	5	- 12.2	-100- 25	60.0
Red Nucleus	7	- 46.0	-100- 0	100.0
Ventral Tegmental Area	4	- 56.0	-100- 10	75.0
Substantia Nigra	2	-100.0		100.0
Postrubral Reticular Formation	2	- 3.5	- 30- 23	50.0
Interpeduncular Nucleus	3	10.3	- 18- 59	66.7
Central Tegmentum-Median Raphe	4	- 33.5	-100- 18	75.0
Pontine Reticular Formation	4	45.0	- 10- 68	25.0

As in the previous study (Thompson, 1976), critical regions for the performance of the appetitively motivated white-black discrimination were defined as those brain sites damaged in rats achieving zero or negative savings scores. Mapping these critical regions on brain diagrams derived from the Massopust (1961) atlas was done in a manner similar to that described elsewhere (Thompson, 1976).

RESULTS

Table 1 presents the mean retention scores for all groups and the percentage of animals from each group that earned zero or negative savings scores.

With respect to original learning, the white-black discrimination acquired under thirst motivation was established much more slowly than that acquired under the motive of escape-avoidance of footshock. Mean errors to criterion for all animals involved in the current study was 23.4. This is to be compared with a mean of 11.9 errors for those 95 animals of the previous study (Thompson, 1976) that learned the same discrimination under an aversive motive. This difference is significant ($p < .01$, two-tailed test).

Retentiveness of the white-black discrimination, on the other hand, does not seem to be as affected by the nature of the motive as is original learning. In the present study, the mean error savings score earned by the controls was 91.2%. This is to be compared with a mean error savings score of 97.0% for the 42 control animals of the previous study that learned the same discrimination with escape-avoidance of footshock as a motive. This difference fell slightly short of statistical significance.

With respect to the savings scores earned by the various brain-damaged animals shown in Table 1, it would appear that those lesion placements producing retention deficits on aversively motivated visual discrimination tasks also produce retention deficits on appetitively motivated visual discrimination tasks. Every brain-damaged group of the current study achieved retention scores which were significantly inferior to those achieved by the control group

($ps < .05$, one-tailed test).¹ It will also be noted that at least 25% of the animals in each brain-damaged group earned zero or negative savings scores. Figures 1, 2, and 3 show subcortical lesions in six rats that

Figure 1. Lesions to the areas of the globus pallidus (top) and entopeduncular nucleus (bottom) in rats earning zero or negative savings scores.

Figure 2. Lesions to the areas of the rostral midbrain reticular formation (top) and substantia nigra (bottom) in rats earning zero or negative savings scores.

earned zero or negative savings scores on the white-black discrimination problem.

Figure 4 compares the critical areas for visual discrimination performance motivated by thirst (obliquely striped areas on the right side of each section) with those for visual discrimination performance motivated by escape-avoidance of footshock (blackened areas on the left side of each section). On the whole, the correspondence from the level of the globus pallidus (Figure 4A) to the level of the pontine reticular formation (Figure 4L) is remarkable.

It should be pointed out that the asymmetrical distributions of critical areas shown in Figures 4D, 4I, 4J, and 4K are not to be interpreted as glaring discrepancies, but rather are probably due to incomplete (or unsuccessful) canvassing of certain subcortical areas with lesions. No animals, for example, were designated to receive lateral geniculate lesions (accounting for the asymmetry in Figure 4D) inasmuch as Lashley (1935) previously reported that

damage to these nuclei abolish appetitively motivated brightness discrimination habits in rats. With respect to the asymmetries noted in Figures 4I, 4J, and 4K, none of the 10 animals receiving discrete two-stage lesions within the ventrolateral aspects of the brain-stem reticular formation survived long enough to complete the retention test; they either died within 2 days after the second surgical procedure or suffered prolonged aphagic-adipsic disorders.²

DISCUSSION

In light of the results of this study, it is reasonable to conclude that the brain mechanisms underlying an appetitively motivated visual discrimination task in rats are not remarkably different from those underlying an aversively motivated visual discrimination task. In all cases studied, lesions to those subcortical sites previously found to impair retention of aversively motivated visual discrimination habits also impair

Figure 3. Lesions to the areas of the red nucleus (top) and median raphe (bottom) in rats earning zero or negative savings scores.

Figure 4. Frontal sections at successive levels of the brainstem are based upon the Massopust (1961) stereotaxic atlas. Obliquely striped areas on right side of each section show composite lesion placements in those rats earning zero or negative savings scores on the appetitively motivated visual discrimination problem, while blackened areas on left side of each section show composite lesion placements in those rats earning zero or negative savings scores on aversively motivated visual discrimination problems. Abbreviations: ac = anterior commissure, cg = central gray, cp = caudoputamen, f = fornix column, gl = lateral geniculate nucleus, gm = medial geniculate nucleus, h = habenula, ic = inferior colliculus, ip = interpeduncular nucleus, lt = lateral thalamus, m = mammillary bodies, mrf = midbrain reticular formation, mt = medial thalamus, p = pons, pp = cerebral peduncle, prf = pontine reticular formation, sc = superior colliculus, st = subthalamus, vm = ventromedial hypothalamus, vt = ventral thalamus.

retention of an appetitively motivated visual discrimination habit. Similar results have been reported at the cortical level: Occipital ablations abolish appetitively (Lashley, 1929) as well as aversively (Horel, Bettinger, Royce, & Meyer, 1966; Thompson, 1960) motivated brightness discriminations in rats.

It is important to note that all of the brain-damaged animals of the present study appeared highly motivated to gain access to water by the 3rd day of the retention test, suggesting that the visual discrimination deficits arising from lesions to those subcortical sites shown on the right side of Figure 4 are not the consequence of a gross decrement in thirst motivation. Seven animals (two with pallidal, one with entopeduncular, one with lateral hypothalamic, two with ventral tegmental, and one with nigral lesions), however, did show a transient disturbance in pushing aside the stimulus cards. (In such cases, the experimenter would displace the card that was initially approached to allow the rat to enter the goalbox.) This disturbance, which has also been observed in brain-damaged animals trained on aversively motivated discrimination tasks (Thompson, 1978), is interpreted as a sensorimotor disorder rather than as a motivational disorder.

As discussed earlier (Thompson, 1976), two major ascending fiber systems are clearly recognizable within the distribution of critical subcortical sites for aversively motivated visual discrimination habits. One of these is the ascending brainstem reticular system, and the other is the nigrostriate (dopaminergic) system. The results of the present study reaffirm the importance of these two ascending fiber systems in the performance of visual discrimination habits. That these two anatomical systems may be significant for nonvisual as well as visual habits is suggested by the distribution of critical subcortical sites for the performance of a vestibulo-kinesthetic (inclined plane) discrimination habit (Thompson, Arabie, & Sisk, 1976), a maze habit (Thompson, 1974), avoidance responses (Thompson, 1978), and latch box tasks (Spiliotis & Thompson, 1973). Electrical stimulation (Kesner & Wilburn, 1974; Routtenberg & Holtzman, 1973) and recording (Olds, Disterhoft, Segal, Kornblith, & Hirsh, 1972) studies also implicate the brainstem reticular formation and nigrostriate systems in the performance of learned activities in the rat.

The functional significance of these anatomical systems in the maintenance of learned responses is uncertain. Contributions related to attention and motor control are in keeping with current neurophysiological views, but it is doubtful that these are the only psychological processes mediated by the activities of the ascending reticular and nigrostriate systems. It is not inconceivable that these two anatomical systems combine to serve a highly complex function in adaptive behavior (see Thompson, 1981).

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NOTES

1. It must not be concluded that lesions placed anywhere within the brainstem induce amnesic effects on the thirst-motivated visual discrimination habit. Eight rats sustaining bilateral one-stage lesions within the medial thalamus or mesencephalic central gray earned savings scores within the range established by the control group.
2. This high mortality rate may be due, at least in part, to the preoperative stress associated with a prolonged water deprivation schedule.

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