RETENTION OF THREE BRIGHTNESS DISCRIMINATIONS BY RATS
FOLLOWING POSTERIOR CORTICAL LESIONS

by

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ABSTRACT

Rats were trained on one of three brightness discriminations. In one task, the discriminanda differed in both luminance and luminous flux. In the second task, the discriminanda differed only in terms of luminous flux. In the third task, the discriminanda differed only in terms of luminance. Following acquisition, half of the animals on each task underwent removal of the striate cortex. Retention tests indicated that a discrimination based on flux cues was relatively undisturbed following striate removal, whereas a discrimination based on luminance cues appeared to be permanently lost. Transfer discrimination tests indicated that deficits other than sensory impairments may follow striate ablation. Results are discussed in terms of sensory and attentional deficits which occur with striate removal.

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Numerous experiments have demonstrated that brightness discriminations can be learned without the striate cortex in the rat (Lashley, 1935b; Thompson, 1960), cat (Smith, 1937), dog (Maquis, 1934), and monkey (Kluver, 1942). However, in the normal animal it is clear that the striate cortex is involved in such learning since removal of this area results in complete loss of a preoperatively learned brightness discrimination (Lashley, 1930, 1935b; Smith, 1937; Bauer and Cooper, 1964; Schilder, 1966; Pasik, Pasik, and Schilder, 1969; Schilder, Pasik, and Pasik, 1971). Some studies, using emitted rather than reflected light (Bauer and Cooper, 1964) or amphetamine therapy (Braun, Meyer, and Meyer, 1966; Jonason, Lauber, Robbins, Meyer, and Meyer, 1970), have not obtained complete loss; however, operated animals were still generally found to be inferior to intact controls.

Two models have evolved to account for the postoperative deficits in performance. Both are based on the finding that normal and operated animals use different cues to solve a brightness discrimination. Although under some special circumstances intact animals may use flux cues (Bauer and Cooper, 1964; Schilder, Pasik, and Pasik, 1967), intact animals normally use some form of pattern vision and/or luminance cues* to solve such discriminations, while operated animals depend upon luminous flux cues* (Kluver, 1942; Bauer and Cooper, 1964; Goodale and Cooper, 1965; Schilder, 1966; Pasik et al, 1969; Bland and Cooper, 1970; Schilder et al, 1971).

Cooper and his coworkers have postulated that while normal animals make at least some use of pattern vision to solve brightness discriminations, operated

* Luminance is defined as the amount of light per unit area of the stimulus. Luminous flux is defined as the total amount of light emitted by or reflected from the stimulus.

animals are unable to utilize pattern cues and essentially have to relearn a discrimination on the basis of a different cue, i.e., flux (Bauer and Cooper, 1964; Goodale and Cooper, 1965; Bland and Cooper, 1970). The evidence cited for this position is twofold. First, the stimulus parameters used in original learning can affect postoperative performance (Bauer and Cooper, 1964). Second, the performance of operated animals is impaired to a greater extent than that of normal animals when stimulus conditions are changed, e.g., with increases in background illumination (Bauer and Cooper, 1964) or decreases in the luminosity differences of the two discriminanda (Lashley, 1930). The two lines of evidence suggest that sensory deficits may account for the postoperative difficulties of operated animals on brightness discriminations.

Hamilton and Treichler (1968) utilized Lashley's (1935b) hypothesis of two visual systems. They postulated that brightness discrimination in the normal animal involves acuity and intensity mechanisms located in the striate cortex. Operated animals have available only a subcortical intensity mechanism and must use essentially different structures, i.e., subcortical areas, to solve such discriminations postoperatively. The evidence supporting this position is twofold. Some researchers (e.g., Fischman and Meikle, 1965) have shown that secondary destruction of some subcortical areas can cause further disruption of a habit previously disturbed by striate removal. In addition, Hamilton and Treichler (1968) found that, although a relevant pattern discrimination facilitated original acquisition of a brightness discrimination, the use of such a cue preoperatively did not appear to affect postoperative performance. The above, together with their finding of no postoperative savings, lead them to suggest that pre- and post-operative learning are essentially independent processes, an idea also advanced by Horel, Bettinger, Boyce, and Meyer (1966) and by Jonason et al (1970). These two lines of

evidence indicate that pre- and post-operative learning are subserved by different and independent neural mechanisms. The necessity of switching from a cortical to a subcortical system following striate removal is therefore presumed to underly postoperative deficits in performance, rather than any sensory deficits which occur following striate removal.

Further research is needed to elucidate the nature of the deficit in performance, particularly in light of some research which cannot be adequately accounted for by either of the two models. For example, Thompson (1969), among others, has demonstrated that some subcortical lesions can result in postoperative deficits similar to those following striate removal. Braun et al (1966) and Jonason et al (1970) have shown that amphetamine treatments can facilitate the reestablishment of a brightness discrimination following striate removal while having no effect on original acquisition in operated animals. They suggested that amphetamine facilitated access to a secondary engram based on flux cues that had been laid down at the same time as a primary engram based on edge-related cues. Striate removal prevented in some fashion access to this secondary engram. These studies imply that both cortical and subcortical regions are involved in original acquisition and argue against both a purely sensory deficits explanation and an explanation postulating independent visual systems subserving pre- and post-operative learning. Lashley (1931) and Bauer and Cooper (1964) have reported that a discrimination based on light vs no light can result in high postoperative savings in rats. Bauer and Cooper (1964) also were able to obtain high savings by the sewing of translucent cups over the eyes of experimental animals. Such a procedure not only would eliminate pattern vision but also probably force an animal to rely on the density of light or flux in order to solve a brightness discrimination. It seems possible that acquisition of a light-no light discrimination may also be

based largely on flux rather than pattern or luminance cues. If such is the case, then it appears that a preoperatively acquired flux discrimination suffers minimal postoperative disruption. Such savings would argue against the notion that normal animals utilize only cortical mechanisms in learning brightness discriminations.

The present experiment is an attempt to test the predictions of the two models on postoperative retention of two brightness discriminations. One group of rats was trained on a luminous flux discrimination. The Bauer and Cooper (1964) hypothesis would predict that the discrimination would not be disturbed by removal of the striate cortex. Since flux is the cue utilized by operated animals, the sensory impairments occurring with striate removal would not affect postoperative performance. Hamilton and Treichler (1968) would predict complete loss of the habit, since striate ablation would remove the cortical mechanisms upon which learning was based. However, they would also predict that the discrimination would be relearned by operated animals in no less than the original number of trials. A second group of animals was trained on a luminance discrimination. Both models would predict complete and permanent loss of the habit postoperatively, since luminance is a cue that striate lesioned animals are unable to utilize. Since the discriminanda were presented in a manner not employed by previous studies examining the deficits following striate removal, an additional discrimination was presented to a third group of rats. In this task, luminance and luminous flux covaried and both were available as cues for solving the discrimination. This was done in an attempt to replicate previous findings with a black-white task (Thompson, 1960; Horel et al, 1966) and with situations using translucent doorways illuminated from behind (Schilder, 1966).

Previous experiments attempting to test flux discrimination in the rat

have used translucent goal box doorways differing in area and illuminated from behind. Differences in flux were obtained by equating luminance values for the two doors (Goodale and Cooper, 1965; Bland and Cooper, 1970; Tees, 1971). The present experiment utilizes point sources as the discriminanda to avoid presenting size as a relevant cue during original learning. Since luminance does not vary with distance while illumination or density of flux falling on a surface varies inversely with the square of the distance (Riggs, 1965), placement of two such sources equated for luminance at different distances from the subject would result in a flux difference for the two sources. Conversely, two sources of unequal luminance placed at predetermined different distances from the subject would result in a luminance difference but equivalence in luminous flux.

METHOD

Subjects

The subjects were 60 naive male Long-Evans hooded rats obtained from Canadian Breeding Farms and Laboratories, Ltd.. They were individually housed in 8 x 7 x 10 in. cages and maintained on ad lib food and water.

Apparatus

Subjects were trained in a two-choice shock avoidance discrimination box. It consisted of a start box (11 x 6 x 5½ in. deep) with a guillotine door, a choice chamber (22 x 18 x 5½ in. deep), and two goal boxes (8 x 8½ x 5½ in. deep). The floors of all chambers were constructed of ¼ in. brass rods, spaced ½ in. apart, center to center. The walls and top of the start box and the walls of the choice chamber were constructed of wood and painted a flat black. A wire grid formed the top of the choice chamber. The side walls and hinged top of the goal chambers were constructed of wood, painted a flat black, and covered with a black velvet cloth. The end walls were of clear Plexiglas. The wooden partition separating the goal boxes extended 4½ in. into the choice chamber and this extension was also painted a flat black. Swinging clear Plexiglas doors provided entrance to the goal boxes.

The grid floors of all chambers were independently wired to a shock generator with a scrambler circuit. Scrambled shock was used in the choice chamber. Unscrambled shock was used in the start box and in the grids in front of the goal boxes, over which the partition extended into the choice chamber. The shock level varied from .14 to .7 ma., depending upon the level needed to elicit avoidance behavior from the particular subject being run. The goal box grids were activated in such a way that a subject would receive shock automatically when he approached the incorrect doorway. To aid recording of responses, a small neon bulb was placed in series with each of the goal box

grids. When a subject stepped onto a wrong grid, thus closing the circuit and receiving a shock, the appropriate bulb would flare. The bulbs were placed below the level of the testing chamber and were out of sight of the subject.

A partitioned box (52 x 18 x 5½ in. deep), similar to that used by Crawford (1935), was constructed to house the stimuli. The side and back walls, floor, dividing partition, and hinged top were constructed of wood, painted a flat black, and covered with a black velvet cloth. The front wall was open. This chamber was placed against the training box so that the open end of the light chambers faced the Plexiglas walls of the goal boxes.

The discriminanda were clear 7 watt bulbs mounted on wooden blocks that had been painted a flat black and covered with a black velvet cloth. A groove was bored down the center of the floor of each light chamber. A small strip of wood was glued to the bottom of each block, such that, when this strip was fitted into the floor groove, the blocks holding the lights were always centered within the light chambers. The cords for the lights were passed through holes bored into the back walls of the chambers. Power sources for the lights consisted of four voltage transformers (two General Radio Variacs and two Superior Electrical Co. of Bristol Powerstats) set at predetermined values. Aside from the two discrimination lights, the only light source within the testing room was a dim red bulb, placed well below the level of the testing chamber, which was used to illuminate the scoring sheets.

Luminance values were measured in nits with a Pritchard Photometer (Photo Research Labs.). Illumination of density of flux readings in lumens per square foot were obtained at the doorways to the goal boxes with a Lightmaster Photometer (Evans Electroselenium, Ltd.). Flux values were calculated by multiplying the obtained readings by the areas of the doorways (16 sq. in.). The black velvet covering in the light chambers and the goal

boxes served to maximally reduce reflection of light from the walls of the chambers. This procedure resulted in illumination readings that followed the inverse square law fairly closely for the first three feet of the light chambers. Beyond this point, readings were somewhat lower than would be expected from the inverse square law. The values used beyond this distance were those obtained, where possible, with the meter rather than the calculated values.

Surgery and Histology

Surgery was performed under sodium pentobarbital anaesthesia. The dorsal surface of the skull was removed from approximately two mm behind bregma to lambda, and from approximately one mm lateral to the sagittal suture to the zygoma. Suction was used to remove the exposed cortical tissue. After completion of the experiment, operated animals were perfused with 0.9% saline followed by 10% formal-saline. Brains were removed and placed in 10% formal-saline for several days. Diagrams were made of the extent of the lesions. Brains were then placed in 15% alcohol for at least 24 hours and then freeze sectioned at 30 microns. Every fourth section was saved, stained with cresyl violet, and examined for cortical and subcortical damage and for retrograde degeneration in the dorsal lateral geniculate nucleus.

General Procedures and Tests

Pretraining procedures were identical for all animals. On all pretraining days, illumination was provided by the two discriminanda to be used in the flux discrimination, placed equidistant from the goal chambers and so equated for both luminance and luminous flux. On Day 1, subjects were placed three at a time into the testing apparatus and allowed to explore it for 15 minutes. On Day 2, subjects were trained to leave the start box within five seconds of the guillotine door being opened and to enter either of the two goal chambers within 20 seconds of entering the choice chamber. Failures were punished with

shock. Criterion was three consecutive non-shocked runs. On Day 3, subjects were again trained to run into the goal boxes. However, the doors to the goal boxes were gradually closed over the first five trials, so that the rats began to learn to push aside a door to enter a goal chamber. Criterion was three consecutive non-shocked runs, all of which required pushing open a fully closed door.

On Day 4, subjects began training on one of the three discriminations. Twenty subjects were run on each task, with no rat being used for more than one task. For all tasks, the stimulus having the higher luminance and/or flux value was the correct stimulus. Each rat was dark-adapted for about 20 minutes before being run. The incorrect doorway was then locked and the grid in front of it activated. Subjects were run for 10 trials a day, with an intertrial interval varying from 90 to 150 seconds. Position of the correct stimulus was alternated according to a Gellerman (1933) series, a total of seven such series being used over consecutive days. Criterion was 18/20 over two days.

Within each task, rats were systematically divided into two groups matched for mean learning scores. One group on each task was subjected to removal of the striate cortex 24 hours after reaching criterion. Following a 14 day recovery period for operated animals and a 14 day resting period for controls, all subjects were rerun on the original discrimination until criterion was reattained. Following this retesting period, all rats were run for a further four days on transfer tests. Ten trials were run on each of these days with the original discrimination alternating with a new transfer discrimination. On transfer trials, both doors were unlocked and no shock was administered for "wrong" responses. The specific transfer discrimination used depended upon the original discrimination and these will be detailed below.

Luminance-luminous flux discrimination. In this task, luminance and luminous flux covaried and both were available as cues for solving the discrimination (LF task). The primary purpose of this task was to find out if the use of the particular discriminanda in this experiment would result in postoperative deficits similar to those obtained with other tasks such as a black-white discrimination (Thompson, 1960; Bauer and Cooper, 1964) or a discrimination involving emitted light with luminance and luminous flux dependent upon doorway area (Schilder, 1966). The luminance and luminous flux values were 13500 nits and .133 lumens respectively for the brighter light and 370 nits and .011 lumens for the dimmer light. The brighter light was 17 in. and the dimmer 9 in. behind the goal box doorways. Transfer tests were run after subjects had completed the relearning series of trials to try and find out whether subjects had employed luminance or flux or both cues to solve the discrimination. Half of the normal and operated animals had the following sequence of transfer tests. On Days 1 and 2 of the transfer series, the original discrimination was alternated with a new discrimination in which the stimuli were equated for luminance but had the same flux values as the stimuli of the original discrimination. On days 3 and 4, the original discrimination was alternated with a new discrimination in which the stimuli were equated for flux but had the same luminance values as the stimuli of the original discrimination. The rest of the subjects had the transfer tests presented in the reverse order.

Luminous flux discrimination. In this task, the luminance values were equated for the two stimuli but the flux values differed (F task). The purpose of this task was to find out whether a discrimination based on flux differences could be learned by normal rats and whether such a discrimination would be lost following removal of the striate cortex. The luminance and luminous flux

values were 3400 nits and .04 lumens respectively for the higher flux light and 3400 nits and .0042 lumens for the lower flux light. The higher flux light was 16 in. and the lower flux light 48 in. behind the goal box doorways. Transfer tests were given following relearning to both groups to try and discover whether the difference in distance between the two lights had contributed to learning. For this purpose, the original discrimination was alternated with a new discrimination in which the stimuli were equated for flux but were unequal in luminance and distance from the goal box doorways.

Luminance discrimination. In this task, luminous flux was equated for the two discriminanda but luminance values differed (L task). The purpose of the task was to find out whether luminance could serve as a cue for the normal rat and whether such a discrimination would be permanently lost following removal of the striate cortex. The luminance and luminous flux values were 13500 nits and .011 lumens respectively for the brighter light and 370 nits and .011 lumens for the dimmer light. The brighter light was 48 in. and the dimmer 9 in. behind the goal box doorways. Transfer tests were again run following relearning in order to find out if the difference in distance of the two stimuli had contributed to learning. The original discrimination was alternated with a new discrimination in which the stimuli were equated for luminance but were unequal in flux and distance from the goal box doorways.

RESULTS

Discrimination Tests

Luminance-luminous flux task. Table I presents median pre- and post-operative error scores for groups on all three tasks. On the LF task, operated animals committed significantly more errors than controls on postoperative retention tests ($U = 21.5$, $p < .025$, one-tailed). However, operated animals obtained significantly lower error scores postoperatively than preoperatively ($U = 7$, $p < .001$, one-tailed), indicating that considerable savings had occurred.

Luminous flux task. Again, operated animals were significantly inferior to controls on retest errors ($U = 9$, $p < .001$, one-tailed). As with the LF task, operated animals showed significant savings in error scores postoperatively ($U = 11$, $p < .01$, one-tailed).

Luminance task. All but three of the operated animals failed to reattain criterion postoperatively, despite being run for twice the number of trials as originally required to attain criterion. One animal committed fewer and two animals more errors than preoperatively.

Transfer Tests

Luminance-luminous flux task. Since there were no significant differences due to the order of presentation of the transfer discrimination tests, the results were combined for analysis. Separate analyses were performed on the luminance and on the flux transfer series. Table II presents median errors on the interspaced original discrimination trials, mean responses to the higher luminance stimulus, and mean position choices on the luminance transfer trials for the operated and control animals. On the luminance transfer series, operated and control animals did not differ in number of errors on those trials on which the original discrimination was presented. Analysis of variance

TABLE I

Median Errors to Criterion Preoperatively (Preop) and Postoperatively (Postop) on the Luminance-Luminous Flux Task (LF), the Luminous Flux Task (F), and the Luminance Task (L) for the Operated (O) and Normal (N) animals.

Task	Group	Preop	Postop
LF	O (n=10)	37.5	7.0
	N (n=10)	37.5	3.0
F	O (n=10)	32.0	7.0
	N (n=10)	33.0	0.0
L	O (n=10)	44.0	105.5*
	N (n=10)	51.0	4.5

* Seven animals did not reattain criterion.

TABLE II

Luminance Transfer Tests on the LF Task: Median Errors on the Original Discrimination Trials (OD), Mean Responses to the Higher Luminance Stimulus (Lu), and Mean Responses to a Preferred Position on the Transfer Trials (P).

Group*	OD	Lu	P
O ₁ (n=5)	2.0	3.0	7.2
O ₂ (n=5)	2.0	4.8	9.4
N ₁ (n=2)	1.5	7.5	5.5
N ₂ (n=8)	1.5	4.7	6.0

* The operated (O) and normal (N) groups have been subdivided into two groups each on the basis of mean responses to the higher luminance stimulus. The subscript 1 refers to those animals responding to one stimulus on at least 65% of the trials; the subscript 2 refers to those animals responding in a random fashion to the stimuli. The maximum number of responses in each column is ten.

indicated that there was no overall differential response to the discriminanda on the luminance transfer trials but there was a significant interaction effect ($F = 6.26$, $df = 1/18$, $p < .025$). Operated animals tended to choose the lower luminance stimulus more frequently than controls. There was also a significant overall response to position on the luminance transfer trials ($F = 13.43$, $df = 1/18$, $p < .005$). The interaction effect approached but did not reach significance ($F = 3.36$, $df = 1/18$, $.10 > p > .05$). The mean response to position on the transfer trials for the operated and control animals (Table II) suggests that operated animals did have stronger position habits than did controls. Control animals tended to respond in a random manner.

Table III presents median errors on the interspaced original discrimination trials, mean responses to the higher flux stimulus, and mean position choices on the flux transfer trials for the operated and control animals. On the flux transfer series, operated and control animals again did not differ in number of errors on those trials on which the original discrimination was presented. Analysis of variance indicated that there was a significant choice of the higher flux stimulus ($F = 15.57$, $df = 1/18$, $p < .005$), but no interaction effect. There was also a significant response to a preferred position on these same trials ($F = 10.15$, $df = 1/18$, $p < .01$), but again no interaction effect.

A Spearman rank-order correlation between position choice and choice of the higher flux stimulus was negative and significant ($\rho = -.66$, $t = -2.5059$, $df = 18$, $p < .025$, one-tailed). A Spearman rank-order correlation between number of correct responses on the interspaced original discrimination trials and choice of the higher flux stimulus of the transfer discrimination was positive and significant ($\rho = .74$, $t = 3.1404$, $df = 18$, $p < .005$, one-tailed). These correlations suggest that a high degree of transfer occurred between the original and the transfer discriminations. Moreover, to the degree that such

TABLE III

Luminous Flux Transfer Tests on the LF Task: Median Errors on the Original Discrimination Trials (OD), Mean Responses to the Higher Flux Stimulus (F1), and Mean Responses to a Preferred Position on the Transfer Trials (P).

Group*	OD	F1	P
O ₁ (n=9)	1.0	8.6	5.8
O ₂ (n=1)	6.0	5.0	10.0
N ₁ (n=9)	1.0	8.7	6.1
N ₂ (n=1)	3.0	6.0	9.0

* The operated (O) and normal (N) groups have been subdivided into two groups each on the basis of mean responses to the higher flux stimulus. The subscript 1 refers to those animals responding to one stimulus on at least 65% of the trials; the subscript 2 refers to those animals responding in a random fashion to the stimuli. The maximum number of responses in each column is ten.

transfer did not occur, animals of both groups responded by position on the transfer discrimination trials.

Luminous flux task. Table IV presents median errors on the interspaced original discrimination trials, mean responses to the nearer stimulus on the transfer trials, and mean position choices on the transfer trials for the operated and control animals. Operated animals were significantly inferior to controls in number of errors on those trials on which the original discrimination was presented ($U = 22.3$, $p < .025$, one-tailed). On the transfer trials, analysis of variance showed that there was a significant overall choice of the nearer stimulus ($F = 10.65$, $df = 1/18$, $p < .001$), but no interaction effect. There was also a significant response to a preferred position on these same trials ($F = 18.03$, $df = 1/18$, $p < .001$), but again no interaction effect.

A Spearman rank-order correlation between choice of the nearer transfer stimulus and choice of position on the transfer trials was negative and significant ($\rho = -.57$, $t = -1.9637$, $df = 18$, $p < .05$, one-tailed). A Spearman rank-order correlation between number of correct responses on the interspaced original discrimination trials and choice of the nearer stimulus on the transfer trials was positive and significant ($\rho = .62$, $t = 2.2171$, $df = 18$, $p < .025$, one-tailed). These two correlations indicate that transfer did occur between the two discriminations. Moreover, to the degree that transfer did not occur, animals in both groups responded to a preferred position on the transfer trials.

Luminance task. Table V presents median errors on the interspaced original discrimination trials, on the transfer tests, mean responses to the further transfer stimulus, and mean responses to a preferred position on the transfer trials for the operated and control animals. Operated animals responded just above chance level on those trials on which the original dis-

TABLE IV

Transfer Test Results on the F Task: Median Errors on the Original Discrimination Trials (OD), Mean Responses to the Nearer Stimulus (NS), and Mean Responses to a Preferred Position on the Transfer Trials (P).

Group*	OD	NS	P
O ₁ (n=4)	1.5	13.5	11.5
O ₂ (n=6)	5.0	11.0	15.7
N ₁ (n=5)	0.0	16.2	11.8
N ₂ (n=5)	3.0	11.0	15.4

* The operated (O) and normal (N) groups have been subdivided into two groups each on the basis of mean responses to the nearer stimulus. The subscript 1 refers to those animals responding to one stimulus on at least 65% of the trials; the subscript 2 refers to those animals responding in a random fashion to the stimuli. The maximum number of responses in each column is twenty.

TABLE V

Transfer Test Results on the L Task: Median Errors on the Original Discrimination Trials (OD), Mean Responses to the Further Stimulus (FS), and Mean Responses to a Preferred Position on the Transfer Trials (P).

Group*	OD	FS	P
O (n=3)**	7.0	10.7	14.0
N ₁ (n=6)	2.0	16.7	12.0
N ₂ (n=4)	3.5	10.8	15.5

* The normal animals (N) have been subdivided into two groups on the basis of mean responses to the further stimulus. The subscript 1 refers to those animals responding to one stimulus on at least 65% of the trials; the subscript 2 refers to those animals responding in a random fashion to the stimuli. The maximum number of responses in each column is twenty.

** Seven animals did not reattain criterion postoperatively and were not given the transfer tests.

crimination was presented. On transfer trials, one operated animal responded randomly and two showed a strong position preference. Normal animals had a median of three errors on the original discrimination trials. A correlated t-test showed a significant choice of the further stimulus on the transfer trials by the intact animals ($t = 3.1845$, $df = 9$, $p < .01$, one-tailed), as well as a significant position choice on these same trials ($t = 4.5435$, $df = 9$, $p < .005$, one-tailed).

A Spearman rank-order correlation between choice of the further stimulus and choice of position on the transfer trials was negative and significant ($\rho = -.64$, $t = -2.3333$, $df = 8$, $p < .025$, one-tailed). A Spearman rank-order correlation between number of correct responses on the interspaced original discrimination trials and choice of the further transfer stimulus was positive and significant ($\rho = .55$, $t = 1.8553$, $df = 8$, $p < .05$, one-tailed). These correlations indicate that for some of the intact animals transfer did occur between the two discriminations. Those animals not showing transfer tended to respond by position on the transfer trials.

Histology

Figure 1 presents diagrams of the extent of cortical damage and corresponding retrograde degeneration in the dorsal lateral geniculate nucleus. All animals sustained damage to callosal fibers underlying the aspirated areas of the cortex, as well as minor invasion of the hippocampus bilaterally. Such subcortical damage did not serve to differentiate between animals on the basis of postoperative performance on any of the three tasks. Most animals suffered subtotal destruction of the striate areas with sparing generally confined to the most posterior margin of the striate cortex. The extent of sparing was not related to postoperative performance on any of the three tasks. Spearman rank-order correlations between striate damage and postoperative performance and

FIGURE 1

Diagrammatic representation of cortical damage and dorsal lateral geniculate nucleus retrograde degeneration for animals on all three tasks. The top two rows present animals learning the LF task; the middle two rows present animals learning the F task; and the bottom two rows present animals learning the L task. Regions that have been blacked out represent areas of cortical damage and geniculate degeneration.

FIGURE 1

between geniculate degeneration and postoperative performance were insignificant for all three tasks. A Spearman rank-order correlation between extent of striate damage and geniculate degeneration was positive and significant ($\rho = .41$, $z = 3.1493$, $p < .001$, one-tailed). Ranks for striate damage were obtained by superimposing diagrams of the cortical lesions over cortical maps based on Kreig's (1946) mapping of the cortical areas.

DISCUSSION

A potential problem in interpreting the present results is the fact that the lesions were generally incomplete, sparing the most posterior portions of the striate areas. However, this does not appear to be of major concern. There was no correlation between striate damage or geniculate degeneration and postoperative performance on any of the three tasks. The three animals who were able to reattain criterion on the L task were among those animals with the greatest amount of damage in that group. The only animal to show perfect savings on the F task had a virtually complete lesion, showing only minimal sparing in the dorso-lateral margin of the right geniculate nucleus. Similarly, animals with minimal sparing in one or both geniculate nuclei reattained criterion on the LF task with error scores below the median for that group. Finally, animals on the LF task had generally more complete damage than animals on the L task. Yet, the LF task animals showed consistently high savings, while seven of ten L task animals (including the five with the least damage) were unable to reattain criterion within the postoperative testing period. Generally, the histological data seems to be consistent with that of Horel et al (1966) and Braun et al (1966) who found no correlation between extent of damage and relearning of an black-white task. Horel et al (1966) concluded that the sufficient lesion for disturbing the habit involved destruction of Lashley's (1932) area critical for pattern vision.

Acquisition of the LF task appears to have been on the basis of the flux rather than the luminance cue or both cues. The high postoperative savings of the operated animals suggests that these animals were utilizing essentially the same cue postoperatively as preoperatively. On the luminance transfer trials, the predominant mode of responding by the intact animals was random, while the operated animals tended to show strong position habits. Although

this indicates different modes of responding by the intact and operated animals on the luminance transfer trials, it also suggests strongly that luminance was not a relevant cue for either group. On the other hand, both groups showed strong transfer from the original discrimination to the higher flux stimulus of the flux transfer discrimination, indicating that flux was a highly relevant dimension for both groups.

Use of the LF task did not results in the type of deficits obtained by previous researchers with a black-white habit or with situations using translucent doorways illuminated from behind (Thompson, 1960; Bauer and Cooper, 1964; Horel et al, 1966; Schilder, 1966). The difference in luminance was of the order of 36.5 to 1 while the difference in flux was of the order of 12 to 1. Since the LF task appeared to have been learned on the basis of the flux cue only, this suggests that for the rat flux may be a more salient cue than luminance. This suggestion is also supported by the faster initial learning of the F task animals than the L task animals. The difference in the flux task was 10 to 1, while the difference in the L task was 36.5 to 1. The lower retest errors for the intact animals on the F task gives additional support to this notion.

The high postoperative savings by operated animals on the F task again supports the notion that a flux discrimination is not greatly disturbed by striate removal. However, the results of the transfer tests are less clear in establishing that flux was the sole cue utilized by the animals in learning the discrimination. On the transfer discrimination trials, four operated and five control animals responded positively to the nearer stimulus. On the original discrimination, the correct stimulus was also the nearer stimulus. It is probable that it was the dimension of depth to which animals were responding on the transfer trials. Lashley (1937) noted that striate rats

seem able to respond to the gross position in space of illuminated objects and Lashley (1931) described three animals with complete striate lesions who were able to accurately jump distances of 20 cm or more, although less reliably than controls. It seems, then, that depth as well as flux may have been used to learn the discrimination and that it was the dimension of depth to which animals transferred their responses on the transfer trials.

As on the F task, rats acquiring the L discrimination may have done so on the basis of depth as well as luminance. On the transfer tests, six intact animals tended to respond strongly to the further stimulus. This was also the location of the correct stimulus on the original discrimination, suggesting that these animals transferred from the original discrimination on the basis of depth differences. It is doubtful that depth was the primary cue in either task. The L task had the greater distance difference between the stimuli (9 : 48 in. vs 16 : 48 in. for the F task), yet, original acquisition was much slower than on the F task. The difference in postoperative retention by operated animals on the two tasks also argues against this possibility.

The three operated animals who were able to relearn the L task may have done so on the basis of flux cues. Although flux was equated at the doorways to the goal boxes, the situation was such that there was a flux difference of 5 : 1 in favor of the higher luminance stimulus at the entrance to the choice chamber from the start box. This would be a difficult but not necessarily impossible discrimination for a striate animal. As on the F task, it is also possible that the depth difference between the stimuli may have been utilized as a cue for relearning. The transfer test results for the operated animals contribute little to an understanding of which was the relevant cue during relearning. All animals performed poorly on the interspaced original discrimination trials as well as on the transfer trials, responding either randomly or

by position on both discriminations. This does not necessarily indicate that the cues present in the transfer discrimination were not utilized by these animals during relearning. Lashley (1930) has shown that the performance of operated animals is impaired by changes in stimulus conditions. He has suggested that this may reflect an impaired ability of striate lesioned rats to adapt to new visual situations. If the operated animals on the L task relearned using a minimal flux cue, then the change to a very relevant flux cue on the transfer discrimination could result in a breakdown in performance, both on the original and the transfer discriminations. Likewise, if they used a depth cue, or both cues, then large changes in stimulus illumination could also affect performance adversely. Some deterioration in accuracy on the interspaced original discrimination trials during transfer testing occurred for both operated and control animals on all three tasks. The LF task groups were the least impaired and these two groups did not differ in the degree to which they became impaired (Tables II and III). This probably reflects the greater similarity between the original and transfer discriminations, particularly on the flux transfer tests, for this task than for the F and L tasks. The transfer discriminations on the LF task maintained at least one of the conditions present during the original discrimination trials. On the F and L tasks, operated animals were more impaired than controls (Tables IV and V). This is consistent with Lashley's (1930) suggestion that operated animals are somewhat impaired in their ability to adapt to new visual situations. There are two possible reasons that a less severe impairment occurred for the F task operated animals than for the L task operated animals. First, the F discrimination was an easier one for the operated animals and therefore less susceptible to disruption. Such differential disruption has been shown for postoperative retention of a light-dark habit by Bauer and Cooper (1964).

Second, the change in overall illumination on the F task transfer trials represented a decrease in overall light levels rather than an increase as in the case of the L task transfer trials.

On all three tasks, there was a negative correlation between choice of position and choice of a particular stimulus on the transfer trials, when at least some animals showed transfer from the original to the new discrimination. There was also a positive correlation between choice of the correct stimulus on the interspaced original discrimination trials and choice of a particular stimulus on the transfer trials when transfer occurred. This suggests that the primary reason why transfer did not occur for all animals was that the performance of some animals on the original discrimination deteriorated because of the introduction of the transfer discrimination. Such deterioration in performance would prevent transfer to a new discrimination.

There is a possibility that the operated animals on the L task were able to utilize the luminance cue. Pasik et al (1969) and Schilder et al (1971) reported that striate lesioned monkeys were apparently able to utilize luminance as a cue. Two possible explanations for their results are that their monkeys may have used either differential distribution of flux or differences in the rate of change in flux to solve the discriminations. However, both of these explanations are weak in view of the excellent transfer obtained by Schilder et al (1971) over three discriminations in which the only constancy was luminance differences. Although this may reflect species differences, the possibility that luminance may serve as a cue for striate lesioned rats seems to be in need of further examination.

The present results indicate that brightness habits based on identical cues for operated and intact animals suffer relatively little disruption postoperatively. Such results argue strongly against the position of

Hamilton and Treichler (1968) that pre- and post-operative learning are subserved by different and independent neural mechanisms. The significant savings on the LF and F tasks contradicts their position that flux discrimination in the normal animal is subserved only by striate acuity and intensity mechanisms, since complete loss should therefore follow striate removal. The evidence that subcortical lesions alone can result in losses similar to those following striate removal (e.g., Thompson, 1969) also contradicts their position. Further, Baden, Urbaitis, and Meikle (1965) have shown that removal of the ectosylvian gyri in cats caused reappearance of the loss of a light-dark habit after it had been lost through successive ablation of the lateral, posterolateral, and suprasylvian gyri. Since removal of the ectosylvian gyri alone did not disturb the habit, this suggests that recovery of the habit after total loss is a function of an interaction between cortical and subcortical areas, rather than a function of the activity of subcortical areas alone.

Superficially, the results appear to support Bauer and Cooper's (1964) contention that the postoperative deficits are due to sensory losses alone. The discrimination data is in agreement with their finding of greater savings on a light-dark task than on a black-white task. However, their hypothesis would predict no loss of a discrimination based on flux cues, while the results of the present experiment show that some postoperative disturbance of the habit does occur. In addition, their hypothesis cannot account adequately for the operates significantly inferior performance to controls on the interspaced original discrimination trials during transfer testing on the F and L tasks. Part of the evidence used by Bauer and Cooper (1964) in support of a sensory deficits hypothesis was the finding that progressive increases in background illumination caused greater impairments in performance

for operates than for normal controls. They interpreted this difference as demonstrating that operated animals were hampered by sensory deficits occurring after striate removal. However, Cooper, Freeman, and Pinel (1967), in a Skinner box situation, found consistently inferior performance by operated animals even at light levels well above threshold. They argued that this does not necessarily reflect sensory deficits since this difference occurred well above threshold, the difference did not increase over decreasing light levels, as would be expected, and operated animals were consistently inferior to controls over several days of testing at baseline levels. Examination of Bauer and Cooper's (1964) Figure 6 suggests that this same argument might apply in the situation of increasing background illumination. This is not to suggest that sensory deficits have not played a prominent role in causing postoperative performance deficits, particularly on black-white tasks and the L task of the present experiment. However, the above analysis suggests that another factor is involved in such deficits.

Krechevsky (1936) has postulated that posterior lesioned rats suffer an attentional deficit. He found that under food reinforcement conditions, operated rats were inferior to controls on original learning of a light-dark habit, when dark was positive. On retention testing, non-shocked operates were again inferior to controls, but this difference decreased considerably for shocked operates. Krechevsky (1936) has suggested that shock heightened attention to the relevant cue in the situation. Lashley (1935a) commented that in successive training to the brighter of two lights, with successive decreases in the luminosity differences between the discriminanda (Lashley, 1930), the performance of operated animals broke down as the difference approached limen. Performance was above chance but never reached errorless criterion. He suggested (Lashley, 1935a) that the variability in performance

obtained might be due to attentional fluctuations. His subsequent rejection of the possibility of attentional deficits (Lashley, 1935b) is based on his assumption that such a deficit would be reflected in slower initial learning by operated animals. Krechevsky (1936) showed that attentional deficits may be minimized under conditions of punishment for errors by shock, a condition which Lashley always used. Krechevsky (1936) also pointed out that normal animals preferred the darker of two stimuli but this preference was reversed in striate lesioned animals. Since Lashley always trained his animals to the brighter stimulus, normal animals would be performing under a handicap which operated animals did not have. Horel et al (1966) have suggested that if this switch in preference is taken into account, operated animals in fact would be inferior in original learning. This has been shown by Krechevsky (1936) under non-shock conditions and by Parker, Erickson, and Treichler (1969) under shock conditions. In addition, Spear and Braun (1969) have shown that the acquisition functions of striate lesioned and normal animals do differ even when responding to the brighter stimulus, and that the difference increases as the difference between the stimuli decreases. Braun et al (1966) and Jonason et al (1970) have been able to facilitate the reestablishment of a black-white habit in rats with amphetamine injections prior to retention testing. They suggested that amphetamine facilitated access to a secondary engram based on flux cues that had been laid down during original learning along with a primary engram based on edge-related cues. It seems possible that amphetamine facilitated attentional processes through general increases in arousal of the operated animals and that this was the basis of access to the secondary engram. Finally, Butter (1969) has shown that monkeys with lateral striate lesions may have a selective attentional deficit. They were not inferior to controls on learning of a bar length discrimination but

were impaired in test situations when irrelevant features were added to the discriminanda. However, they were impaired only above a criterion of 70% correct, suggesting attentional rather than sensory or learning deficits. Similar results can be found on the LF and F tasks of the present experiment. Operated animals in both tasks did not differ from controls on retest scores up to a criterion of 16/20. It was only beyond this criterion level that operated animals were inferior to controls, suggesting again attentional rather than sensory or learning deficits.

There was a successive deterioration in accuracy on the interspaced original discrimination trials during the transfer test series over the LF, F, and L tasks of the present experiment. Rather than reflecting increases in conditions that could accentuate sensory deficits, this appeared to reflect increases in the difference between the original and transfer discriminations. Presumably, the greater the difference, the more likely the overall situation is to confuse operated animals, particularly if there is present an attentional deficit. Such confusion is likely to interact with an attentional deficit to yield greater general impairment. The deterioration in performance does not seem to reflect increases in learning difficulty over the three tasks, since this order was F, LF, and L, both for original learning and for retention scores of intact animals.

An alternative hypothesis has been suggested by Cooper et al (1967). They have suggested that the primary function of visual cortex may be to impose an organization over other regions of the brain involved in visual processes. Under such an interpretation, removal of the visual cortex might well be expected to result in performance deficits such as those found in the present experiment on retention testing of operated animals on the LF and F tasks, and explained above on the basis of attentional deficits. Their explanation

might be applied equally well to the other data cited in support of an attentional deficits model. There seems in fact to be no crucial difference between the two hypotheses. An attentional deficit might well be a reflection of an impairment in the ability to appropriately organize sensory input.

In summary, it does not seem likely that cortical and subcortical mechanisms form different and independent systems for the solution of brightness discriminations. The primary deficit in most previous studies appears to have been a sensory one, in that normal animals were able to utilize a cue which operated animals were not able to utilize. However, the present results suggest that an additional attentional deficit or an impairment in the ability to organize visual input may also result from striate removal.

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