EFFECTS OF SEQUENTIAL LESIONS OF THE VISUAL CORTEX ON RELEARNING OF PATTERN OR BRIGHTNESS DISCRIMINATIONS IN THE RAT

by

HELEN BARBAS

B.A., Newark State College, 1972

A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Psychology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1974

Approved by:

Major Professor

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ACKNOWLEDGEMENTS

I thank Dr. P. D. Spear for his advice and guidance, and Drs. J. Frieman and J. C. Mitchell for their aid and helpful criticisms. I would also like to thank E. J. Holland for many helpful discussions.

This research was supported in part by a National Institute of Health Grant EY01170 to Dr. P. D. Spear, by a National Institute of Health Training Grant MN08359 and by a Biomedical Sciences Support Grant 08S1 from the National Institute of Health.

GENERAL INTRODUCTION

Recovery of function following damage to the central nervous system has been demonstrated, (Lashley, 1931; Horel, Bettinger, Royce and Meyer, 1966), but the underlying mechanism involved has not been discovered yet. One of the factors which enhances relearning of a certain task following brain damage, is the temporal spacing of the damage in two or more stages. It has been well documented that serial lesions to the brain result in less detrimental behavioral consequences than simultaneous bilateral lesions (Ades and Raab, 1946; Stewart and Ades, 1951; Thompson, 1960; Rosen, Stein and Butters, 1971; Stein, Rosen, Graziadei, Mishkin and Brink, 1969; Finger, Marshak, Cohen, Sceff, Trace and Niemand, 1971; Glendenning, 1972; Petrinovich and Bliss, 1966; Petrinovich and Carew, 1969).

In view of the enhancing effects of sequentially occurring damage, the present study investigated the effects of sequential lesions to the visual cortex of rats on relearning of a pattern and a black-white task. The purpose of the present study is twofold: a. To investigate whether sequential lesions to the visual cortex will make it possible for rats lacking visual cortex to learn a pattern discrimination; and b. To demonstrate whether the sequential lesion effect demonstrated with successive unilateral lesions is general. Two black-white studies using successive bilateral lesions have been designed for this purpose.

Improved recovery of brightness discrimination following unilateral lesions as compared with simultaneous bilateral lesions of the visual cortex has been well documented in the rat (Thompson, 1960; Glendenning, 1972; Petrinovich and Bliss, 1966; Petrinovich and Carew, 1969). Serially lesioned rats relearn the discrimination with savings, while rats with single-stage bilateral lesions show a loss of the discrimination.

Relearning of pattern discrimination habits following bilateral damage to the visual cortex of rats has been confined to tasks where differential contour cues are available to the animal (Cowey and Weiskrantz, 1971; Mize, Wetzel and Thompson, 1971; Lewellyn, Lowes and Isaacson, 1969). Pattern discrimination habits have not been shown to recover in visually decorticated rats when stimuli in which contour cues as well as total and local luminous flux cues are eliminated (Lashley, 1931; Horel, Bettinger, Royce and Meyer, 1966; Thompson, 1969; Braun, Lundy and McCarthy, 1970).

Since sequential lesions have been shown to enhance recovery in many contexts and in different species (Ades and Raab, 1946; Stewart and Ades, 1951; Thompson, 1960; Rosen, Stein and Butters, 1971; Stein, Rosen, Graziadei, Mishkin and Brink, 1969; Finger, Marshak, Cohen, Scheff, Trace and Niemand, 1971; Glendenning, 1972; Petrinovich and Bliss, 1966; Petrinovich and Carew, 1969), they may also facilitate relearning of a pattern discrimination task in which contour cues are eliminated. The purpose of the present study is to determine if sequential lesions will make it possible for rats

lacking visual cortex to perform a horizontal-vertical pattern discrimination, a task which in the past has proved insoluble by rats lacking visual cortex (Lashley, 1931; Horel et al, 1966; Thompson, 1969; Braun et al, 1970).

METHOD

Subjects

The subjects were 20 male Long-Evans hooded rats, 90-120 days old at the beginning of the experiment. They were housed in individual cages with ad libidum food and water.

Apparatus and training procedure

A two-choice shock avoidance box similar to that described by Thompson and Bryant (1955) was used for discrimination training. The apparatus was 10 cm. wide at its narrowest end (the start box), with the width increasing steadily to 30 cm. at the choice point. The start box (20 cm. long) was separated from a choice box by a black plexiglas guillotine door which could be lifted by the experimenter to begin a trial. The choice box (40 cm. long) and a goal box (30 cm. long) were separated by two stimulus doors which could be knocked down by subjects to enter the goal compartment. The floor of the start and choice compartments consisted of a stainless steel grid which could be electrified. A 5 cm. section of the grid immediately in front of each stimulus door could be electrified independently from the rest of the grid. A fluorescent lamp mounted 12.7 cm. above the choice doors provided the only illumination during testing.

The stimuli were 9.0 cm. square plexiglas doors with 4 black (.03mL) and 4 white (.95mL) horizontal (positive stimulus) versus vertical stripes, 1.125 cm. wide. The stimuli

were placed against a black (.04mL) surround. Stimulus brightness was measured using an S.E.I. photometer (Salford Electrical Instruments). Total luminous flux and amount of contour were equal in the two stimuli. Position of the horizontal (positive) and vertical doors was varied from left to right on each trial according to a Gellerman series. Each stimulus also was rotated 180° from trial to trial according to a second Gellerman series, in order to prevent a border from being consistently black or white. Thus consistent trial to trial local flux cues also were eliminated.

On day 1 of the experiment the subjects were allowed 25 minutes of free exploration in the apparatus with no doors present. On day 2 the subjects were given 18 pretraining trials to escape and avoid shock by knocking down gray plexiglas doors and running into the goal compartment. During pretraining no more than three successive responses were allowed to be made to one side and an equal number of responses were made to each side. This was accomplished by locking the door and charging the grid on the favored side. Discrimination training began on day 3. On each trial the subject was required to run from the start box into a choice compartment and into the goal box by knocking down the positive stimulus door. Foot shock of .2 - .4 ma. was administered if the subject failed to leave the start box within 5 seconds or if it failed to make a choice within 30 seconds. An error was originally defined as a trial in which a subject's feet came in contact with the electrified grid 5 cm. in front of

the negative stimulus door. It was observed, however, that rats could push either door with their nose without stepping on the 5 cm. charged grid in front of the negative stimulus door. In order to prevent subjects from using these tactile cues to gain safe access to the goal box, intermittent shock was introduced and an error was recorded whenever a subject's nose approached within 5 cm. of the negative stimulus door. This slight change in procedure affected 6 subjects, 3 in each group, and was made after 175 trials during the second retention test for these subjects (see procedure below). This procedure was then adopted for the remaining rats for all training procedures. Following each trial the subject was removed from the goal box and transferred to a cage for an intertrial interval of at least 90 seconds. The stimulus doors were removed after each trial in order to keep auditory cues constant. The stimuli were also washed frequently in order to eliminate olfactory cues. The rats were run in squads of 6, with 3 rats from each group. Twenty-five trials were given each day until a criterion of 18/20 correct responses was achieved.

Surgery and Histology

Visual cortex removal was performed under Equi-Thesin (Jensen-Salsbery Labs.) anesthesia, .3ml./100 gms. injected intraperitoneally. An incision was made through the skin along the midline, and a bone defect was made over the intended area of the lesion for each group. The cortex was removed by aspiration after removal of the overlying meninges. In each

hemisphere, the intended lesion extended from the posterior tip of the occipital pole to 4.5 mm. anterior from lambda, and 1.5 mm. from the midsagittal suture to 7 mm. laterally. This was intended to include all of areas 17, 18 and 18a according to the cytoarchitectural study of Krieg (1946) and all of the primary and extraprimary visual areas according to the electrophysiological studies of Adams and Forrester (1968), Montero (1973), and Montero, Rojas and Torrealba (1973). Postoperatively the subjects were injected with 100,000 units of bicillin (Wyeth Labs. Inc.) intramuscularly, and were returned to their home cages.

At the end of the experiment the subjects were administered a lethal dose of Equi-Thesin and were perfused through the heart with .9% saline followed by 10% formolsaline. The brains were removed from the skull and the lesions were drawn to scale on standard diagrams of the dorsal view of the rat brain. The brains were then embedded in celloidin and sectioned at 30 micra. Every fifth section through the dorsal lateral geniculate nucleus was mounted and stained with cresyl violet. Retrograde degeneration in the dorsal lateral geniculate muclei was assessed.

Procedure

The subjects were randomly assigned to two equal groups of 10 subjects each. One group received a two-stage visual cortex lesion involving one hemisphere at each stage; this group is referred to as successive unilateral (SU). The second group received a one-stage bilateral visual cortex

lesion which involved both hemispheres; this group is referred to as bilateral (B). A summary of the exact sequence of experimental procedures is shown in Table 1.

Following acquisition of the pattern discrimination task the SU group was subjected to removal of the visual cortex of the right hemisphere. Ten days following surgery for the SU group, both groups were retrained to criterion (R_1). Additional overtraining trials were given to equalize the number of training trials for all rats. Each rat received a total of 50 trials during R_1. Following R_1 both groups were subjected to surgical procedures. For the SU group the lesioned area included the visual cortex of the left hemisphere. The B group received a one-stage lesion involving the visual cortex of both hemispheres. At this time the total extent of the lesioned area was identical for the two groups. Ten days following surgery all subjects were retrained to an 18/20 criterion or until 550 trials, whichever came first.

Table 1

Schedule of Experimental Procedures

		DAYS				
GROUPS	N	1-6	7	17-18	19	29
B	10	A	-	R_1*	V	R_2
SU	10	A	v	R_1*	v	R_2

Abbreviations:
A: Acquisition
R_1: First retention test
R_2: Second retention test
V: Bilateral visual cortex lesion
v: Unilateral visual cortex lesion
*: Overtraining to total of 50 trials

RESULTS

Histological

The lesion size was measured for each rat from diagrams which were drawn to scale from the rat brains (Figure 1). The median lesion size for the left and right hemispheres was 28.19 mm. square and 27.89 mm. square, respectively, for the SU group, and 27.28 mm. square and 25.56 mm. square, respectively, for the B group. Wilcoxon's Matched Pairs Test revealed no statistically significant asymmetry of the lesion extent between the right and left hemispheres for either group ($p > .05$). Since no lesion asymmetry was found, the lesion size of the right and left hemispheres was then averaged for each subject, and the two groups compared. The median lesion size was 28.04 mm. square for the SU group, and 26.42 mm. square for the B group. No significant difference with regard to lesion size was found ($U = 43$).

Diagrams of the extent of retrograde degeneration in the LGNd for individual subjects of the two groups are presented in Figure 1. Seven of the subjects in the bilateral group and seven of the subjects in the successive unilateral group had complete retrograde degeneration of the LGNd bilaterally, and these lesions were judged to be complete. In three of the subjects in each group a small region of scattered healthy cells was observed in two or more consecutive sections. The density of these cells was always less than in the normal LGNd. However, these regions were conservatively considered

Figure Caption

Figure 1. Dorsal view of the brain of each subject showing scale drawings of the visual cortex lesions. Also included are diagrams indicating the extent of retrograde degeneration in the LGNd of each brain. Black in the LGN diagram indicates complete retrograde degeneration. In cases where scattered healthy-appearing cells were present, the locus in which the scattered cells appeared is shown by striations in the LGNd diagrams. In no case was there localized sparing with normal cell density of cells in the LGNd. For reference to the learning data in Table 2, each subject number is indicated to the lower left of each brain. (Scale in mm.)

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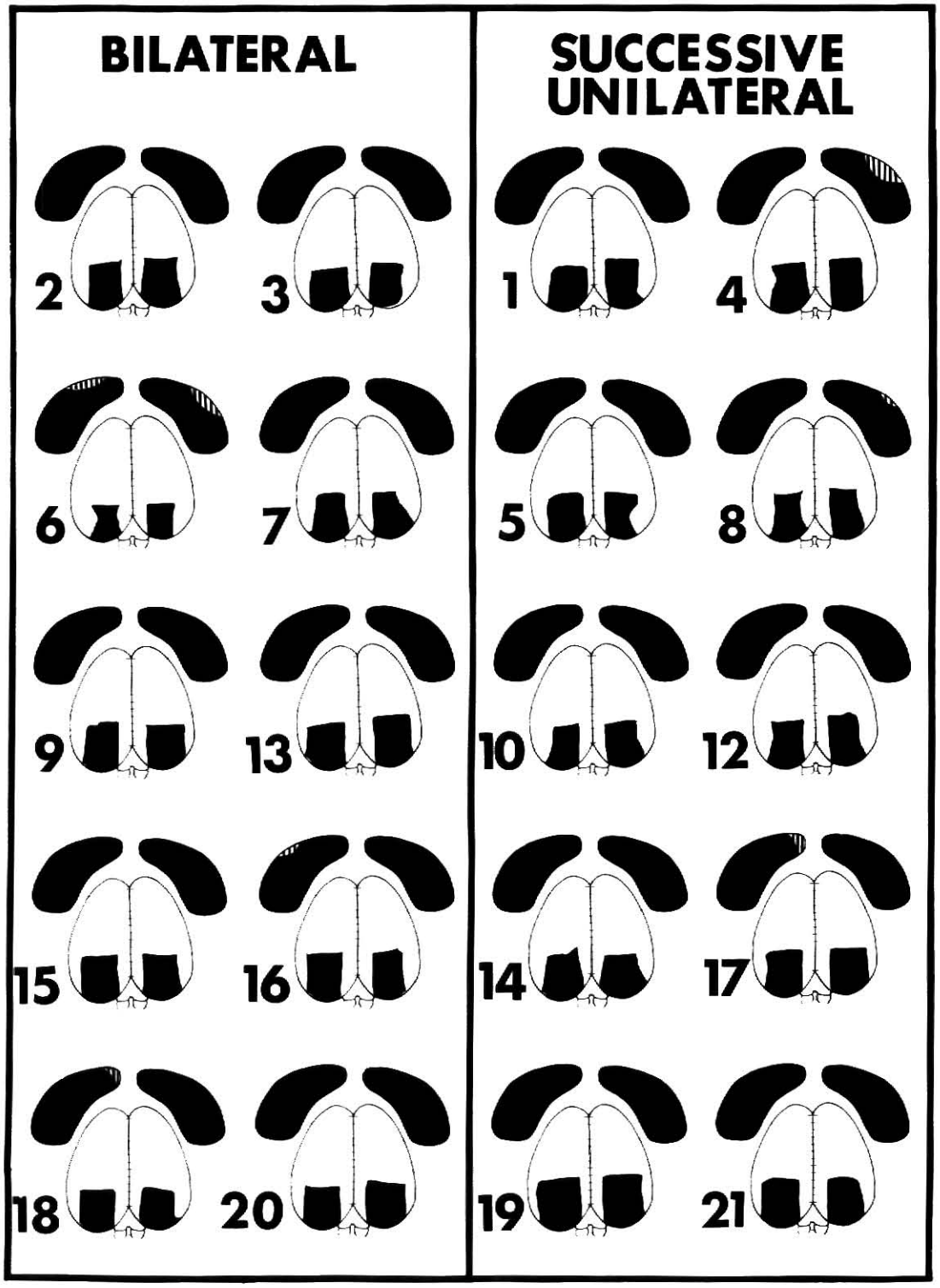
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to represent possible sparing of visual cortex. Otherwise, these rats showed complete retrograde degeneration of the LGNd. The areas of scattered cells are represented by stripes in the LGN drawings of Figure 1. Completely degenerated areas are represented in black.

Behavioral

Table 2 presents the number of errors and trials required for learning and relearning the pattern discrimination task to the 18/20 criterion for individual subjects in the two groups. All statistical comparisons were made with Mann-Whitney U test, two-tailed.

For preoperative acquisition no significant differences were found between the two groups for either trials to criterion or number of errors to criterion, ($U = 47.5$ for trials, and $U = 49$ for errors).

Retention 1 criterion levels were reached by both groups with considerable savings (Table 2). However, the SU group required a significantly greater number of trials to reach criterion on R_1 than the bilateral group. This was true for both trials to criterion ($U = 9.5$, $p < .02$) and number of errors to criterion ($U = 9.5$, $p < .02$). The R_1 test compares the retention of the successive group after a unilateral lesion with that of the bilateral group prior to any lesion. The bilateral group is, therefore, a normal control group at this stage. Therefore, it is concluded that the unilateral visual cortex ablation produced a slight retention deficit.

Table 2

Trials and errors required to reach criterion for preoperative acquisition, first retention test, and second retention test on the horizontal versus vertical stripes discrimination task. Scores include the trials and errors in the criterion block.

	Acquisition		Retention 1		Retention 2*	
Group	T	E	T	E	T	E
Bilateral						
2	48	19	19	1	550	328
3	40	9	18	0	550	323
6	98	27	19	1	550	333
7	58	19	18	0	550	284
9	47	16	19	1	550	323
13	57	16	20	2	550	328
15	37	10	19	1	550	306
16	48	12	20	2	550	318
18	51	15	19	1	550	274
20	44	14	18	0	550	308
Median	48	15.5	19	1	550	320.5
Successive Unilateral						
1	76	20	20	2	398	179
4	45	14	26	5	237	97
5	48	12	24	4	220	86
8	66	25	46	9	550	289
10	45	13	28	7	177	71
12	48	15	32	8	536	220
14	45	13	21	3	448	159
17	46	14	25	4	290	122
19	44	13	29	4	492	168
21	111	34	18	0	270	106
Median	47	14	25.5	4	344	140.5

*training was discontinued after 550 trials

Retention 2 scores indicated a marked loss of the habit following the bilateral visual cortex lesion for subjects in the B group, and the second unilateral lesion for subjects in the SU group. None of the bilateral subjects relearned the discrimination within 550 trials, more than 10 times the number of trials required in original learning. Further, only one of these subjects showed any improvement above chance performance within this number of trials. On the other hand, nine of the 10 successive unilateral subjects were able to relearn the pattern discrimination to the 18/20 criterion, requiring a median of 344 trials. The two groups differed in both trials to criterion ($U = 5$, $p < .002$), and number of errors to criterion ($U = 2$, $p < .002$). Figures 2 and 3 present representative learning curves during R_2 for three rats in the B group and three in the SU group.

Additional training

It has been shown previously (Spear and Braun, 1969) that with sufficient training under the proper conditions, cats with total removal of the visual cortex were able to learn a pattern discrimination between stimuli equated for total luminous flux and amount of contour, and in which no local flux cues were available. With this in mind, an attempt was made to determine if rats with one-stage total bilateral removal of the visual cortex could relearn the pattern discrimination task if given sufficient training.

Figure Caption

Figure 2. Representative R_2 learning curves for 3 bilateral subjects. Percent correct choices in successive 25-trial blocks are plotted. The first curve shows the only bilateral subject which showed improvement within the 550 trial training limit. The other 2 curves present typical chance performance of these subjects.

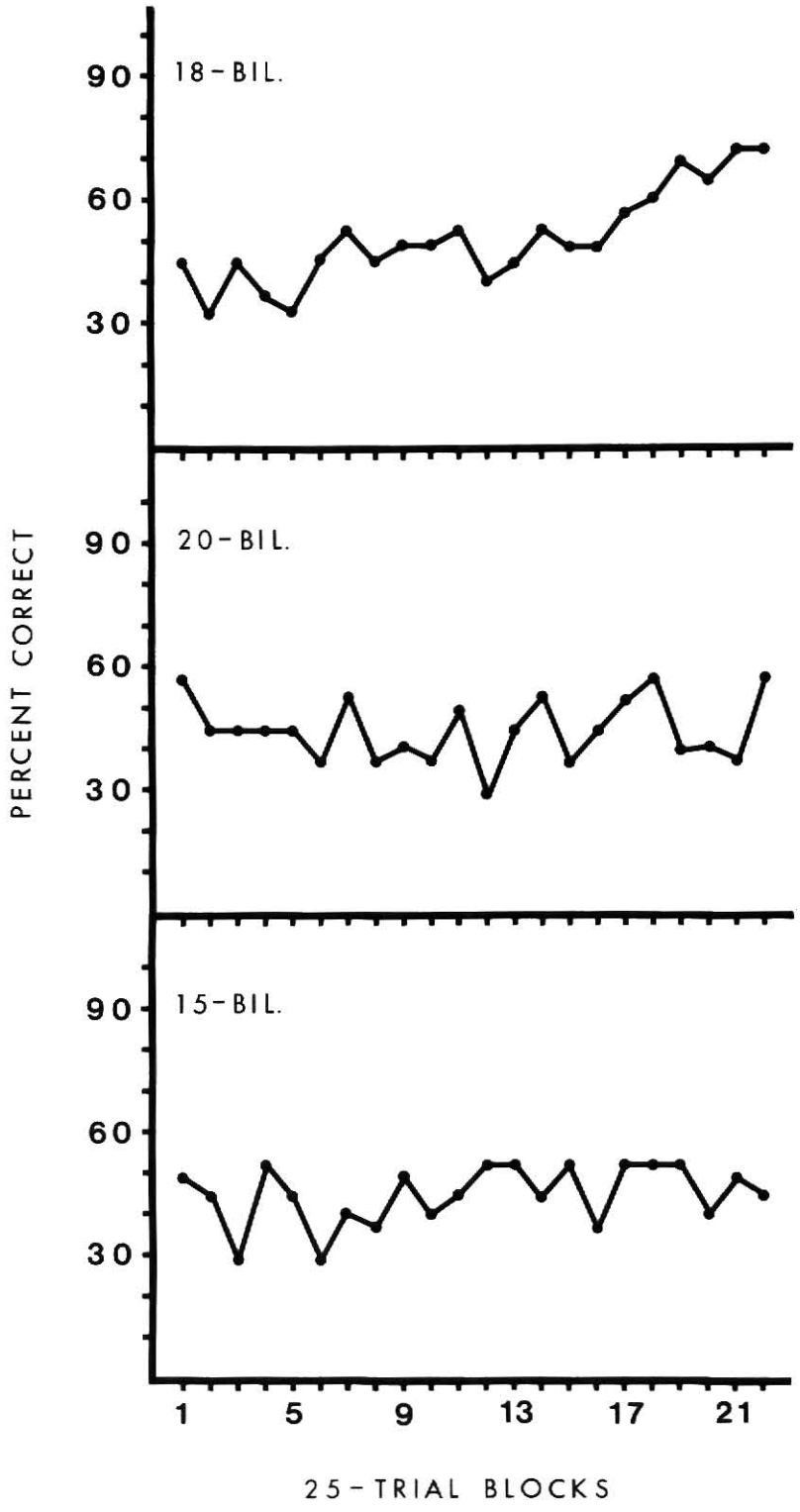
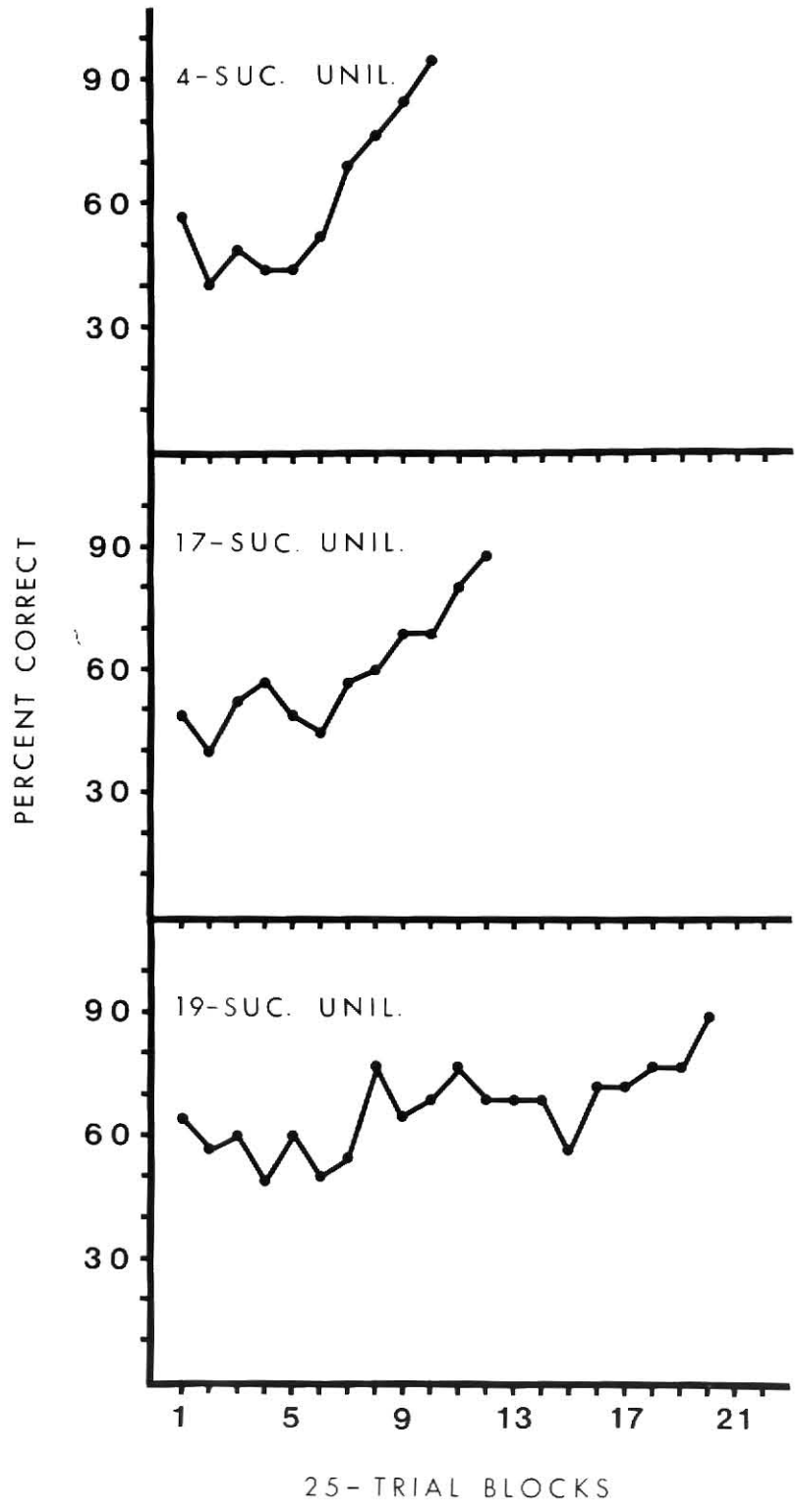

18-BIL.
20-BIL.
15-BIL.
90
60
30
PERCENT CORRECT
1
5
9
13
17
21
25-TRIAL BLOCKS

Figure Caption

Figure 3. Representative R_2 learning curves of the successive unilateral subjects. Percent correct choices in successive 25-trial blocks are plotted. The last point on each curve includes some of the criterion (18/20 correct) trials, and thus, includes fewer than 25 trials in some cases.


4-SUC. UNIL.
17-SUC. UNIL.
19-SUC. UNIL.
90
60
30
PERCENT CORRECT
1
5
9
13
17
21
25-TRIAL BLOCKS

Four bilateral subjects were given 300 additional training trials beyond the 550 trial limit of R_2. Two of these animals relearned the discrimination to criterion within this additional training period (rat 20: 790 trials and 393 errors; rat 18: 551 trials and 274 errors). One subject, (rat 13) showed some improvement in performance to 76% correct responding but did not reach preoperative criterion levels within the additional 300 trials. The fourth subject (rat 15) did not show any improvement within the additional 300 trials.

DISCUSSION

Previous studies have failed to demonstrate recovery of a pattern discrimination task following removal of the posterior neocortex in the rat when total flux, contour, and systematic local flux cues were eliminated in the stimuli (Lashley, 1931; Horel et al, 1966; Thompson, 1969; Braun et al, 1970). Relearning of the discrimination by the successive unilateral subjects may be attributed to the widely documented sequential lesion facilitation effect shown with other tasks in different species and in various brain regions (Ades and Raab, 1946; Stewart and Ades, 1951; Rosen et al, 1971; Finger et al, 1971; Thompson, 1969; Stein et al, 1969; Glendenning, 1972; Petrinovich and Carew, 1969; Petrinovich and Bliss, 1966). However, relearning of the discrimination by rats with one-stage bilateral visual cortex lesion implies that other factors, besides the sequential lesion one, may contribute to the recovery, and may affect both groups of subjects.

One factor which may be important in the relearning of the pattern discrimination task may be the extensive training used in the present experiment. Previous investigators have typically defined "nonlearning" as 300 trials or less (Braun et al, 1970; Horel et al, 1966; Thompson, 1969; Lashley, 1931). In the present study the median learning score was 344 trials for the successive group, and 670.5 trials for the two bilateral subjects which relearned the discrimination. That

extensive training may be an important factor in recovery of a pattern discrimination task has been previously shown in visually decorticated cats (Spear and Braun, 1969) and rats (Cowey and Weiskrantz, 1971; Lewellyn et al, 1969). If training was discontinued at 300 trials in the present study, the results with the bilateral subjects would agree with previous findings (Lashley, 1931; Horel et al, 1966; Braun et al, 1970; Thompson, 1969); however, the successive unilateral subjects would still exhibit superior performance.

Another factor which may be important in recovery of function following damage to the brain is the time between the initial damage to the brain and R_2 training. In the present experiment the successive group received their first ablation 12 days before the bilateral group. It was also observed that the two bilateral subjects which relearned the discrimination did so in a median of 37 days following their bilateral lesion. The median learning time for the successive unilateral subjects was 36 days following their initial unilateral lesion. The present data suggest that the length of time since the initial injury may play a crucial role in the subsequent recovery. The role of time on recovery has been discussed by Isaac (1964) for a black-white task. Isaac showed an interaction between sensory stimulation during the interoperative period, in the subsequent recovery of an avoidance response in serially lesioned rats. Recovery was facilitated when sensory stimulation such as light and noise was provided during a 12-day interoperative interval, and was

retarded in the absence of such stimulation. However, lengthening the interoperative interval by two days facilitated recovery in the absence of light and noise. Thus the time element since initial damage may play a role in the recovery in addition to sensory stimulation or training (Thompson, 1960; Kircher et al, 1970; Glendenning, 1972), and in addition to any special mechanisms induced by sequentially occurring damage per se. While the present data do not separate the role of time since injury and the effects of additional training, they illustrate the need for further experimentation to clarify this issue.

Another factor which may have been responsible for the relearning of the pattern discrimination task in the present experiment may be the size of the lesion. An attempt was made to confine the lesion to the visual cortex as it was electrophysiologically defined by Montero (1973); Montero et al (1973); Adams and Forrester (1968), and according to the cytoarchitectural study of Krieg (1946). It is possible that the area surrounding the visual cortex, and which has been typically ablated along with the visual cortex in the past, may be involved in the recovery. This has been shown to be the case for cats (Wood, Spear and Braun, 1974). Cats with bilateral removal of the visual cortex followed by suprasylvian cortex ablations showed a more severe deficit on a horizontal-vertical pattern discrimination task when compared with cats lacking visual cortex alone. The present data suggest that the failure of past investigators in finding recovery of a

pattern discrimination task may be due to the extent of their lesion. The suggestion that the lesion size may be an important factor in recovery of a pattern discrimination can also be made from the Cowey and Weiskrantz (1971) study in which recovery of pattern discrimination was found following a lesion confined to the visual cortex alone. The present study establishes that rats lacking the striate area, as evidenced by complete degeneration in the LGNd, as well as the extrastriate area (areas 18 and 18a) can relearn a pattern discrimination task. This is contrary to an earlier belief originally held by Lashley (1931) which stated that the striate area is essential for the acquisition of a pattern discrimination task when total luminous flux was equated in the stimuli. The present data agree with the Cowey and Weiskrantz (1971) and the Mize et al (1971) findings which demonstrated relearning of a pattern discrimination task when luminous flux cues were absent, and they further extend relearning to a task in which contour cues are also eliminated.

EXPERIMENT TWO. BLACK-WHITE

When posterior neocortical ablations are performed in two stages rats require a fewer number of trials to relearn a black-white discrimination following the second ablation than is required by rats with bilateral one-stage posterior neocortical lesions. The sequentially lesioned rats relearn the discrimination with considerable savings, while the single-stage rats show a loss of the habit (Thompson, 1960; Glendenning, 1972).

Relearning of a brightness discrimination following removal of the posterior neocortex indicates that either extrastriate cortical areas, or subcortical areas can support the brightness discrimination. The view that subcortical mechanisms are involved in the recovery of the discrimination has been held by Lashley (1931) and by Horel, Bettinger, Royce and Meyer (1966) who demonstrated relearning of a brightness habit following total decortication in the rat. The above studies imply that at least two different visual mechanisms can support brightness discrimination habits: a visual cortical mechanism is implicated in preoperative acquisition and accounts for loss of the habit following removal of the posterior neocortex, and another mechanism is involved in subsequent relearning of the discrimination. Although Lashley's (1931) data, and Horel et al (1966) study suggest that subcortical mechanisms may be involved in the

relearning of a brightness discrimination in the totally decorticated rat, the possibility that extrastriate cortical areas are implicated in the recovery in cases where the damaged area is confined to the visual cortical area, cannot be ruled out.

The mechanism involved in the relearning of the discrimination following posterior decortication and the one involved in preoperative acquisition have been shown to follow a different course. Whereas normal rats show a preference for the darker stimulus when they are initially faced with a black-white discrimination, posteriorly decorticated rats show a preference for the brighter stimulus (Kreschevsky, 1936; Horel et al, 1966; Parker, Erickson and Treichler, 1969; Parker and Treichler, 1973). Normal animals are, therefore, initially handicapped in a situation where the dark stimulus is negative, (which has classically been the case), but are able to show superior performance when more stringent criteria are required (Horel et al, 1966; Spear and Braun, 1969).

It has been suggested (Stein et al, 1969) that improved recovery in sequential lesions is due to a neural reorganization during the interoperative period. A critical factor for sparing of the black-white habit in successively lesioned rats is the presence of practice between two unilateral lesions. Practice, presumably, facilitates reorganization of an extrastriate visual mechanism. Serially lesioned rats who receive interoperative training show superior performance to rats

which are either subjected to simultaneous posterior ablations, or to ones subjected to successive unilateral posterior ablations without interoperative training (Thompson, 1960; Glendenning, 1972; Kircher, Braun, Meyer, and Meyer, 1970).

Studies which have demonstrated savings in serially lesioned rats in brightness discrimination tasks, have all employed lesions involving one posterior cortical hemisphere followed by lesions to the other. The question may be asked whether the improved recovery following successive unilateral lesions to the brain is a general effect of sequentially occurring damage, or if it is unique only to lesions occurring sequentially in opposite hemispheres. The purpose of the present study is to investigate the generality of the sequential lesion phenomenon demonstrated with successive unilateral lesions by using successive bilateral lesions.

METHOD

Subjects

The subjects were 32 male Long-Evans hooded rats, 90-120 days old at the beginning of the experiment. They were housed in individual cages with ad libidum food and water.

Apparatus and Training

The apparatus and training procedures were the same as those used for Experiment 1, and they are fully described above.

In the present experiment the stimuli were 9.0 cm. square plexiglas black (.04mL) and white (1.01mL) doors, placed against a black (.04mL) surround (measured with an S.E.I. photometer). Position of the white (positive) and black doors was varied from trial to trial according to a Gellerman series. The rats were run in squads of 6. Each squad included subjects from two or all three experimental groups. The subjects were given 25 trials a day until a criterion of 18 out of 20 correct responses was achieved.

Surgery and Histology

Surgery was performed under Equi-Thesin (Jensen-Salsbery Labs.) anesthesia, .3ml./100 gms. injected intraperitoneally. An incision was made through the skin along the midline, and a bone defect was made over the intended area of the lesion. The cortex was removed by aspiration after removal of the

overlying meninges. Three different types of visual cortex lesions were performed. The first, termed unilateral, extended from the posterior tip of the occipital pole to 4.5 mm. anterior from lambda, and 1.5 mm. from the midsagittal suture to 7 mm. laterally. This lesion included all of cytoarchitectural areas 17, 18, and 18a (Krieg, 1946), and all of the primary and extraprimary visual cortex according to the electrophysiological data of Adams and Forrester (1968); Montero (1973); and Montero, Rojas and Torrealba (1973). This lesion was produced in one hemisphere only. In the second type, termed bilateral, both hemispheres were lesioned in one stage, and the lesion in each hemisphere extended over the same area as that described for the unilateral lesion. The third type of lesion was termed partial bilateral. In one hemisphere, the lesion was intended to cover the medial portion of the visual cortex, extending 1.5 mm. from the midsagittal suture to 4 mm. laterally, i.e. the width of the lesion was 2.5 mm. and had the same dimensions anteriorly and posteriorly as the above mentioned groups. This area includes the projection of the temporal visual field onto striate cortex as described by Montero (1973) and Montero et al (1973), and it includes all of Krieg's (1946) area 18 and the medial half of area 17. The partial bilateral lesion also included the lateral part of the other hemisphere. The area included in the lateral portion extended from 4 mm. lateral to the midsagittal suture to 7 mm. laterally, i.e. the width of the lesion was 3 mm. and had the

usual anterior and posterior dimensions. This area represents the nasal visual field projection in striate cortex (Montero et al, 1973) and it includes the lateral part of area 17 and all of area 18a (Krieg, 1946). Note that the total amount of cortex ablated in the partial bilateral lesion is exactly the same as in the unilateral lesion, and also that the same composite areas of visual field projection in primary and extraprimary cortex are affected in each lesion.

A diagram of the lesion intent for each group is graphically shown in Figure 4.

Postoperatively the subjects were injected with 100,000 units of bicillin (Wyeth Labs, Inc.) and were returned to their home cages.

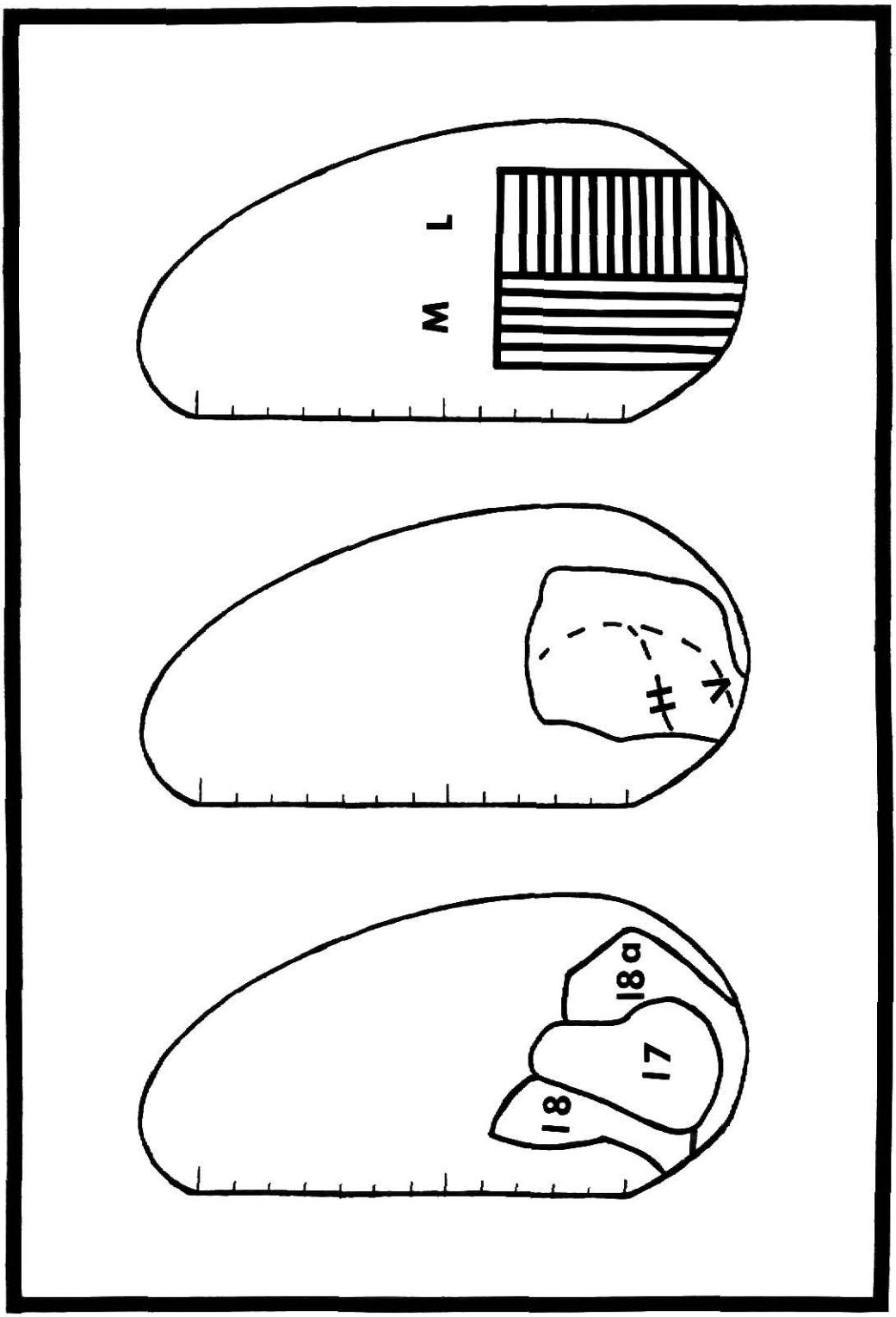
Histological procedures were the same as those described in Experiment.1.

Procedure

The subjects were randomly assigned to three groups of 10 animals in each group with the exception of the successive bilateral group in which 12 subjects were assigned. One group received a two-stage visual cortex lesion involving one hemisphere at each state; this group is referred to as successive unilateral (SU). The second group received a one-state bilateral visual cortex lesion which involved both hemispheres; this group is referred to as bilateral (B). A third group received a two-stage visual cortex lesion involving the medial portion of one hemisphere and the lateral portion of the contralateral hemisphere at each stage; this group is

Figure Caption

Figure 4. Diagrams showing the extent of the visual cortex as described by Krieg (1946; left), and by Montero, Rojas and Torrealba (1973; middle). The extent of the visual cortex in the present experiment is shown at right. Scale in mm. H: horizontal meridian; V: vertical meridian; M: medial visual cortex; L: lateral visual cortex.


M
L
18a
17
18

referred to as successive bilateral (SB). A summary of the exact sequence of experimental procedures is shown in Table 3.

Following acquisition of the black-white discrimination task the SU group and the SB group were subjected to surgical procedures. The first lesion for the SU group involved the right visual cortex lesion described above. For the SB group the partial bilateral lesion was administered, including the medial portion of the right hemisphere, and the lateral portion of the left hemisphere. Ten days following surgery both groups were retrained to criterion (R_1). Additional overtraining trials were given to equalize the number of training trials for all rats. All rats received a total of 50 trials during R_1. Two animals from the SB group were randomly selected after the first stage lesion, and these animals did not receive a second lesion, so that the extent of the neocortical damage and lateral geniculate degeneration might be assessed following a single partial bilateral lesion. Following R_1 all 3 groups were subjected to surgical procedures. For the SU group a unilateral lesion was performed in the left hemisphere. For the SB group a second partial bilateral lesion was given which included the remaining visual cortex of each hemisphere. The B group received a lesion which involved the visual cortex of both hemispheres in one stage. At this time, the extent of the lesioned area was identical in all three groups. Ten days following surgery all subjects were retrained to an 18/20 criterion.

Table 3

Schedule of Experimental Procedures

		DAYS				
GROUPS	N	1-6	7	17-18	19	29
B	10	A	-	R_1*	V	R_2
SU	10	A	v	R_1*	v	R_2
SB	12**	A	vb	R_1*	vb	R_2

*overtraining to a total of 50 trials

**Two animals from this group were randomly selected after R_1 and these animals did not receive a second lesion, so that the extent of the neocortical damage and LGN degeneration might be assessed after the first stage lesion.

Abbreviations:
A: Acquisition
R_1: First retention test
R_2: Second retention test
V: Bilateral visual cortex lesion
v: Unilateral visual cortex lesion
vb: Partial bilateral visual cortex lesion

RESULTS

Histological

The lesion size was measured for each rat from diagrams which were drawn to scale from the rat brains (Figure 5). The mean for the left and right hemispheres was 28.58 mm. and 27.8 mm. square, respectively, for the B group; 26.73 mm. and 27.98 mm. square for the SU group; and 27.38 and 29.25 mm. square for the SB group. Wilcoxon's Matched Pairs Test revealed no statistically significant asymmetry of the lesion extent between the right and left hemispheres for any of the three groups. Since no lesion asymmetry was found, the lesion size of the right and left hemispheres was then averaged for each subject, and the three groups were compared. The mean lesion size was 28.2 mm. square for the B group, 27.3 mm. square for the SU group, and 28.3 mm. square for the SB group. One-way analysis of variance showed no significant differences among the three groups with regard to lesion size.

Diagrams of the extent of retrograde degeneration in the LGNd for individual subjects of the two groups are presented in Figures 5 and 6. Six of the subjects in the B group, eight of the subjects in the SU and eight of the subjects in the SB group had complete retrograde degeneration of the LGNd bilaterally, and these lesions were judged to be complete. In three subjects in the B group and two subjects in each of the SB and SU groups, a small region of scattered healthy cells

Figure Caption

Figure 5. Dorsal view of the brain of each subject in the B and the SU groups showing scale drawings of the visual cortex lesions. Also included are diagrams indicating the extent of retrograde degeneration in the LGNd of each brain. Black in the LGNd diagrams indicates complete retrograde degeneration. White indicates sparing in the LGNd with normal cell density. In cases where scattered healthy-appearing cells were present, the locus in which the scattered cells appeared is shown by striations in the LGNd diagrams. Percent savings scores for trials is shown in the lower left of each brain for R_1, and in the lower right for R_2. Scale in mm.

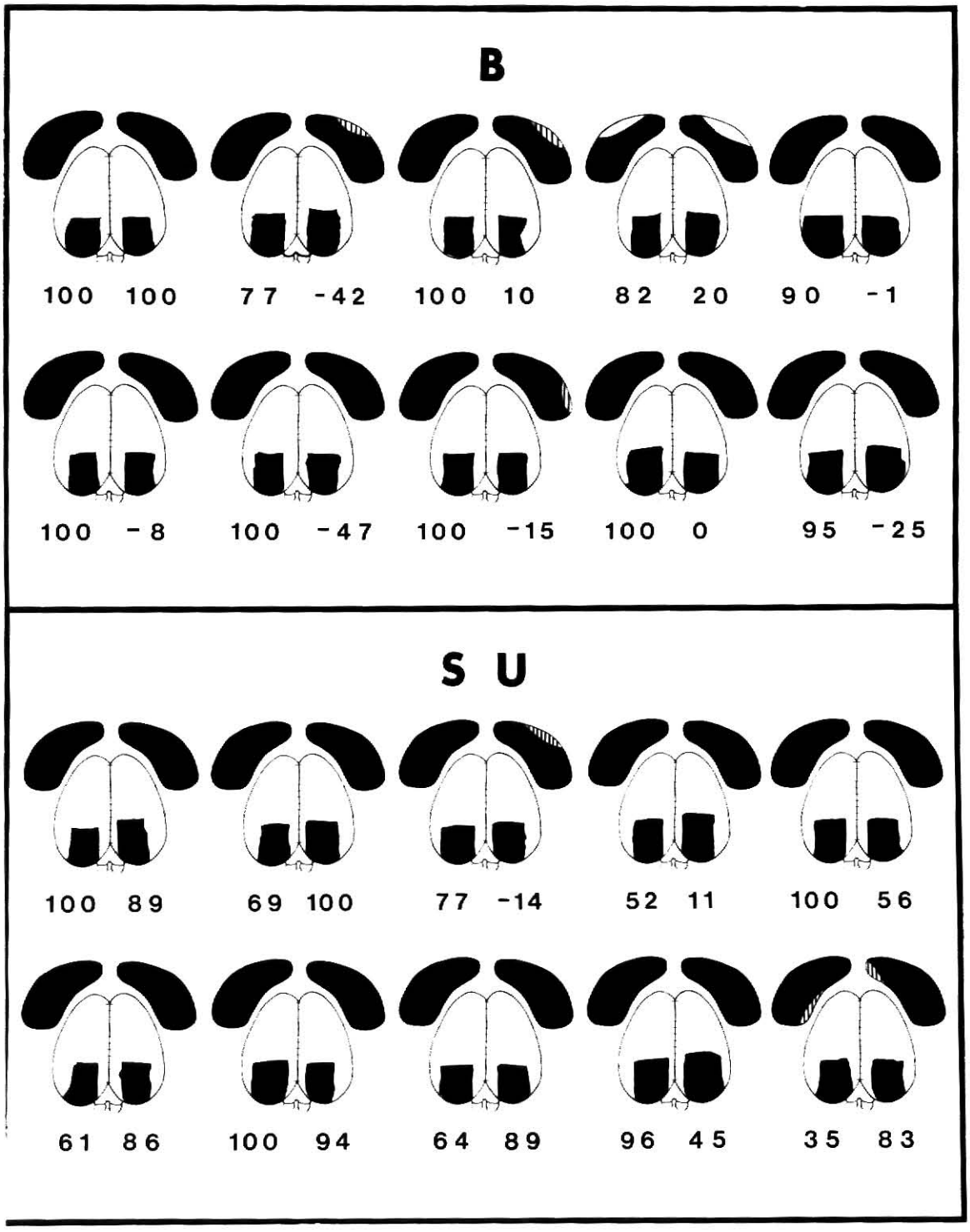
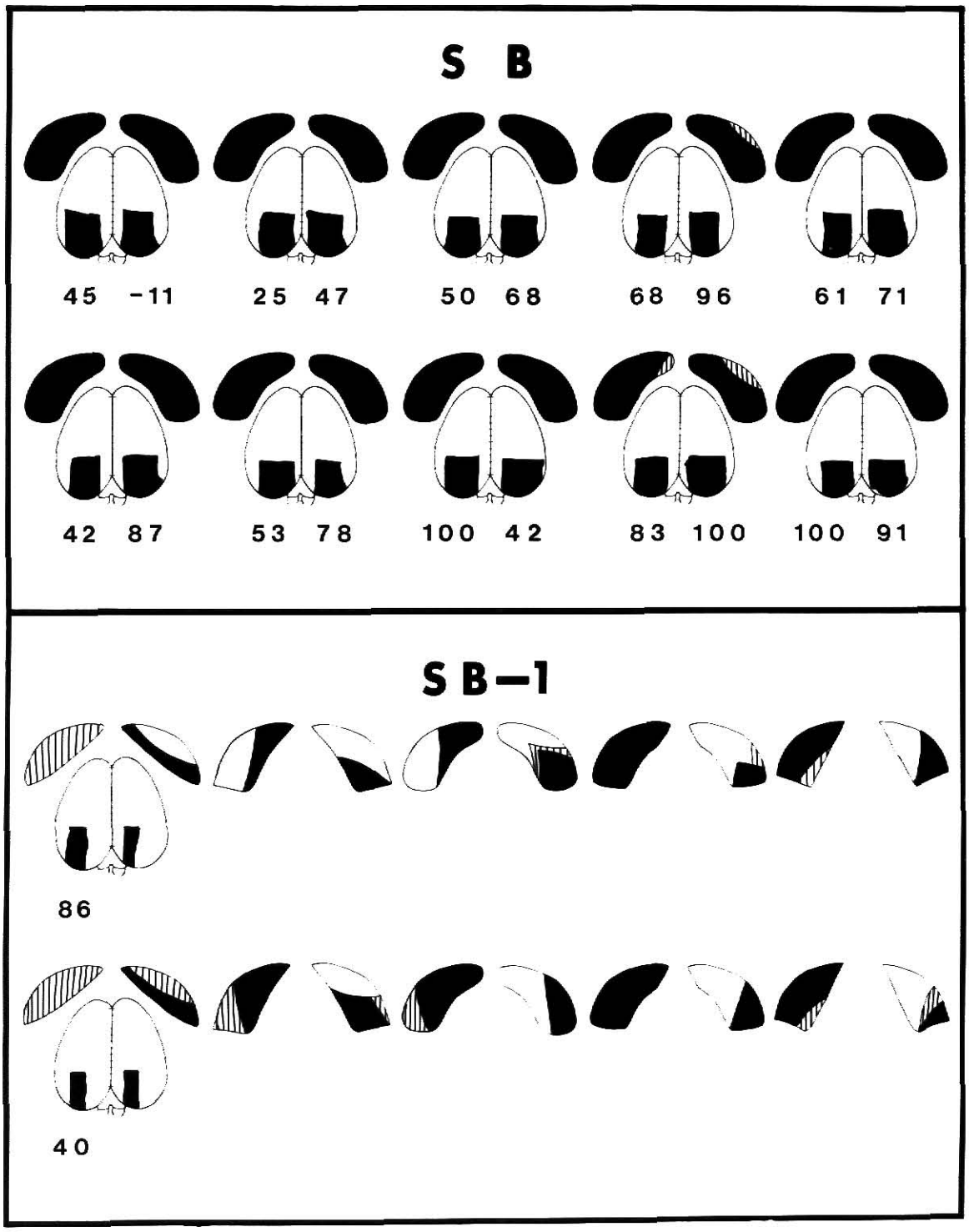

B
100 100
77 -42
100 10
82 20
90 -1
100 -8
100 -47
100 -15
100 0
95 -25
S U
100 89
69 100
77 -14
52 11
100 56
61 86
100 94
64 89
96 45
35 83

Figure Caption

Figure 6. Dorsal view of the brain of each subject in the SB group showing scale drawings of the visual cortex lesions. Also included are diagrams indicating the extent of retrograde degeneration in the LGNd of each brain. For the two brains from the SB group which received only the first stage lesion (SB-1) five geniculate section diagrams are included. These diagrams show the degeneration from anterior LGNd sections (left) to more posterior LGNd sections (right). Black in the LGNd diagrams indicates complete retrograde degeneration. White indicates sparing in the LGNd with normal cell density. In cases where scattered healthy-appearing cells were present, the locus in which the scattered cells appeared is shown by striations in the LGNd diagrams. Percent savings scores for trials is shown in the lower left of each brain for R_1, and in the lower right for R_2. Scale in mm.


S B
45 -11
25 47
50 68
68 96
61 71
42 87
53 78
100 42
83 100
100 91
SB-1
86
40

was observed in two or more consecutive sections. The density of these cells was always less than in the normal LGNd. However, these regions were conservatively considered to represent possible sparing of visual cortex. Otherwise, these rats showed complete retrograde degeneration of the LGNd. One subject in the B group had a small crescent of localized sparing with normal cell density. Otherwise, this rat showed complete retrograde degeneration of the LGNd.

The two brains from the SB group which received only the first stage of a partial bilateral lesion are shown in Figure 6. When the ipsilateral medial aspect of the visual cortex was ablated areas of degeneration were encountered in the medial region in anterior sections, and ventrally in the nucleus in posterior sections. When the ipsilateral lateral visual cortex was ablated areas of degeneration were encountered generally in the dorsal part of the nucleus. All other areas in these brains showed normal cell density. These data are consistent with Lashley's (1934b) degeneration data, and the Montero, Brugge, and Beitel (1968) visual field projection data on the LGN of the albino rat.

Behavioral

Table 4 presents the number of trials and errors required to reach the 18/20 correct criterion for acquisition, R_1 and R_2 for the three groups in the experiment. The results are also presented in the form of average acquisition or retention functions in Figures 7 and 8. These functions show the number of trials it took subjects in each group to reach successive

Table 4

Mean trials and errors required to reach criterion for pre-operative acquisition, R_1 and R_2, as a function of the lesion employed. Savings scores for trials are included for R_1 and R_2 tests. The trial scores do not include the criterion block.

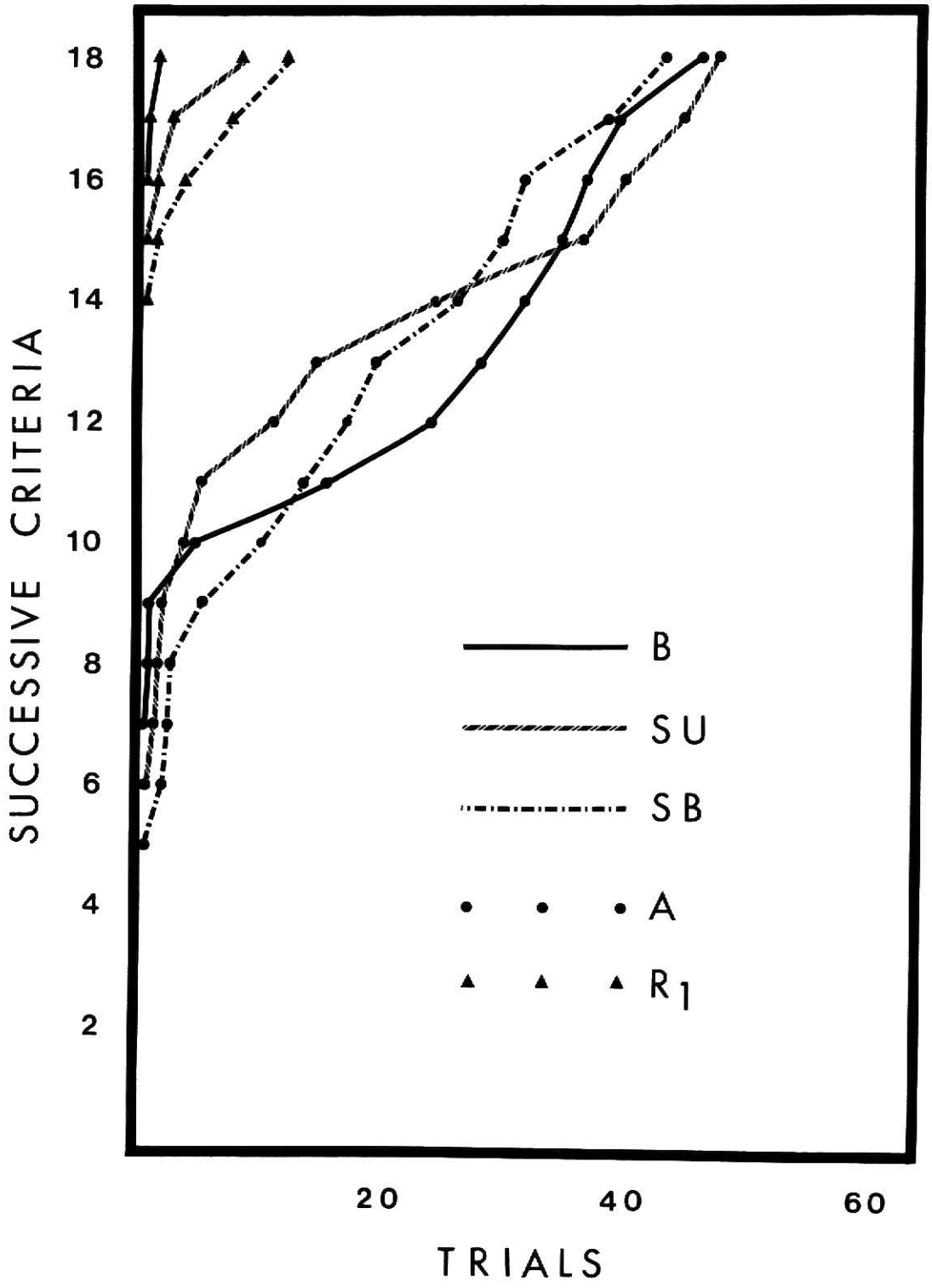
		Acquisition		Retention 1			Retention 2		
Group	N	T	E	T	E	%S(T)	T	E	%S(T)
B	10	46.2	23.0	1.4	0.6	94.4	60.3	22.4	-0.8
SU	10	47.8	22.6	8.5	2.5	75.4	14.5	5.6	63.9
SB	12*	45.0	21.8	12.3	3.7	62.7	12.7	5.4	66.9

*Two animals from this group were randomly selected after R_1, and these animals did not receive a second lesion, so that the extent of the neocortical damage and LGN degeneration following one-stage partial bilateral lesions might be assessed after the first-stage lesion. Therefore, only 10 subjects were included at R_2.

Savings scores were computed by subtracting the appropriate retention trials (R_1 or R_2) from the number of trials to acquisition (A), and dividing by the sum of the particular retention trials and trials to acquisition. The resulting saving scores were converted to percentages by multiplying by 100: (A-Ri/A+Ri)(100).

Figure Caption

Figure 7. Original acquisition and P_1 functions for the 3 experimental groups. I through 18 successive criteria are along the ordinate; number of trials required to reach each successive criterion is along the abscissa. See text for explanation of the computation of each point on the curve.


18
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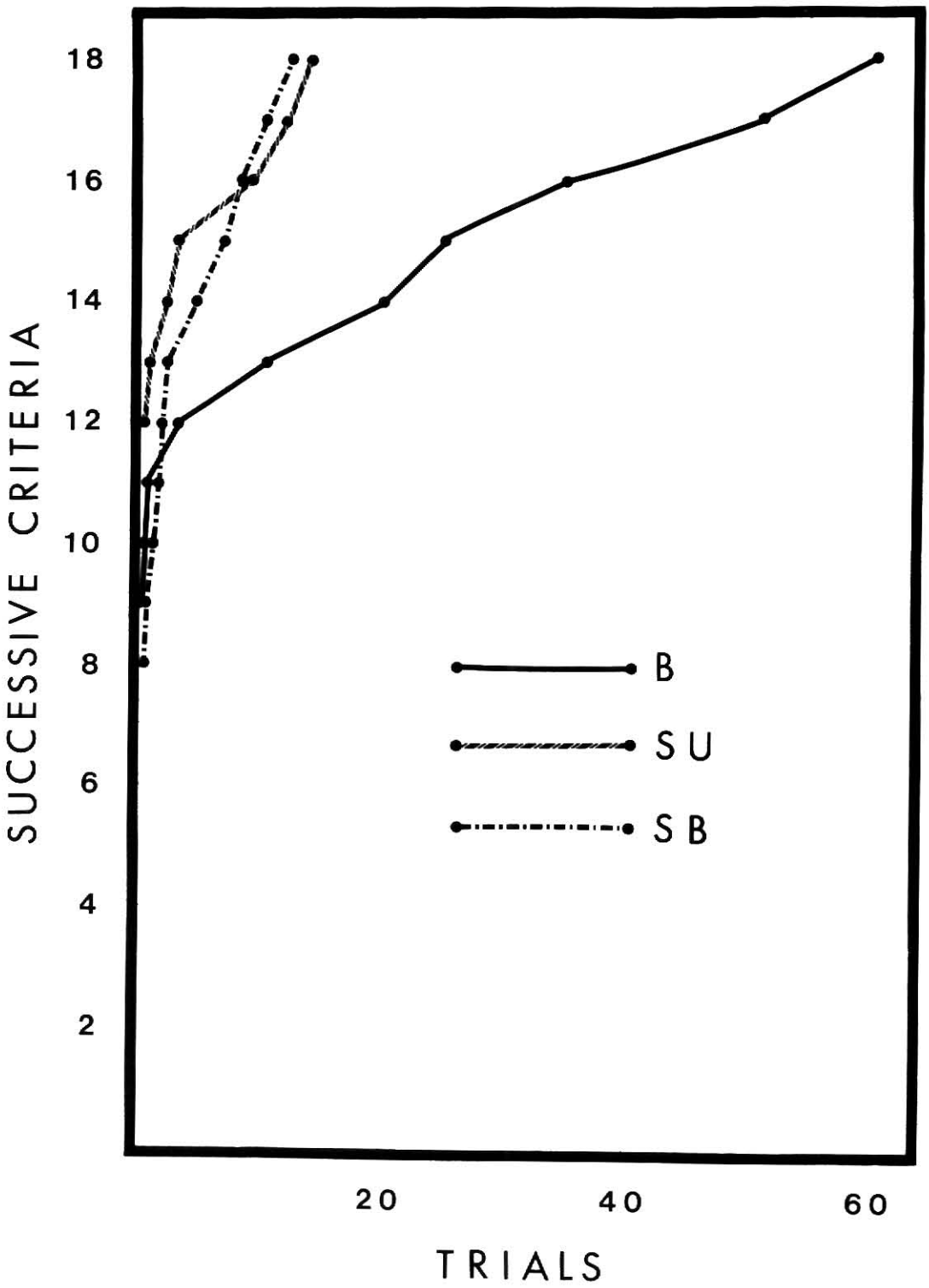
SUCCESSIVE CRITERIA
B
SU
SB
A
R1
20
40
60
TRIALS

Figure Caption

Figure 8. R_2 functions for the 3 experimental groups. 1 through 18 successive criteria are along the ordinate; number of trials required to reach each successive criterion is along the abscissa. See text for explanation of the computation of each point on the curve.


SUCCESSIVE CRITERIA
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criteria of 1 through 18 out of 20 correct responses. The number of trials required to reach the block of 20 trials in which the subject made 1 through 18 correct responses was determined for each subject. The criterion block of 20 trials was not included in the scores. Computation of each point on the curve was obtained by averaging the scores within the group for each criterion. A one-way analysis of variance was used for statistical analysis of preoperative number of trials to the 18/20 criterion, and savings scores for R_1 and R_2. All statistical comparisons were made using Newman-Keuls tests.

Figure 7 presents the acquisition functions for the three groups. For preoperative acquisition no significant differences were found among the groups in either trials ($F = .13$, $p > .05$) or errors ($F = .12$, $p > .05$) to reach the 18/20 criterion.

Figure 7 also presents R_1 functions for the three groups. All groups reached criterion levels at R_1 with considerable savings over original learning. A t-test for dependent groups showed that the number of trials required to reach criterion at acquisition differed significantly from the number of trials at R_1 for all groups ($p < .001$). An analysis of variance of savings scores at R_1 indicated significant differences among the groups for savings scores ($F = 6.5$, $p < .01$). Newman-Keuls comparisons showed no significant differences between the two successive groups. However, the SU group and the B group differed significantly ($p < .05$), and the SB and

B group also differed significantly ($p < .01$). The R_1 test compares the retention of the successive groups after a partial visual cortex lesion, with that of the B group prior to any lesion. The bilateral group is, therefore, a normal control group at this stage. Therefore, it is concluded that the partial visual cortex ablation produced a slight retention deficit.

Figure 8 presents R_2 functions for the three groups. The analysis of variance indicated significant differences among the groups for savings scores ($F = 10.09$, $p < .01$). Newman-Keuls comparisons showed no significant differences between the SU and SB groups. However, both the SU and SB groups differed significantly from the B group in savings scores ($p < .01$). A t-test for dependent groups showed that both successive groups reached the 18/20 correct responses criterion in significantly less trials at R_2 than at acquisition ($p < .001$). However, no significant differences were found between acquisition trials to criterion and R_2 trials to criterion for the B group ($p > .05$). It is concluded that the successive groups reach R_2 criteria with savings, whereas the B group shows a loss of the black-white habit.

DISCUSSION

The present data confirm and replicate previous findings which have demonstrated the facilitative effects of successive lesions on recovery of brightness discrimination tasks (Thompson, 1960; Glendenning, 1972; Petrinovich and Bliss, 1966; Petrinovich and Carew, 1969). Successive unilateral subjects reached preoperative criteria with considerable savings at R_2, but bilateral subjects showed a loss of the habit. Successive bilateral subjects also showed considerable savings at R_2, much like the successive unilateral subjects. It is concluded that sequential ablation of the same amount of cortical tissue and the same visual field projection results in savings whether each stage in the ablation involves one or both visual cortical hemispheres.

The partial bilateral lesion included an equal amount of cortical tissue, and the same visual field projection areas as the unilateral lesion in order to control for any differential effects of the part of the visual field projection removed. This was achieved by ablating the lateral portion of the visual cortex in one hemisphere, and the medial portion of the visual cortex of the contralateral hemisphere. However, as a consequence, the cortical tissue ablated in each hemisphere was qualitatively different, since the lateral portion of the lesioned cortex includes the nasal visual field projection in striate cortex, and the medial portion of the lesioned

cortex receives projections from the temporal visual field. It is possible that the two areas are differentially involved in a black-white discrimination task. It is known that the lateral visual cortex contains the central visual field projection (Adams and Forrester, 1968; Montero et al, 1973). It is possible that this part of the visual cortex plays a crucial role in the acquisition of the black-white habit. If this is true, ablation of the medial portion included in the first-stage partial bilateral lesion may have been inconsequential in the obtained successive effect. That is, the successive bilateral lesion used in the present study may functionally have been a successive unilateral lesion. In order to determine conclusively the generality of the sequential lesion effect, it is necessary to separate the possible differential effects of the lateral and medial portions of the visual cortex on a black-white discrimination task. Therefore, a second experiment was conducted which included groups of rats receiving a lesion of the medial portion of both visual cortical hemispheres at the first stage, and the lateral portion of both visual cortical hemispheres at the second stage, and vice versa.

EXPERIMENT THREE. BLACK-WHITE

The present experiment investigated the effects of successive lesions on a black-white discrimination task when bilaterally symmetrical lesions were performed. One successive bilateral group (ML) received a first stage lesion which included the medial portion of the visual cortex of both hemispheres. The second stage lesion for this group included the lateral portion of both visual cortical hemispheres. A second group (LM) received the above lesions in the reverse order. If the lateral portion of the visual cortex is solely responsible for the discrimination, differences should be expected between the ML and the LM groups at R_1. According to this hypothesis, the LM group should behave like a bilateral group following ablation of its lateral, and presumably, critical cortex. These animals, would, therefore, show a loss of the habit at R_1, and show normal retention at R_2. In addition, the ML group should demonstrate perfect retention of the habit at this time, and show a loss at R_2. A second possibility is that the involvement of the medial and lateral visual cortex may be different for a black-white discrimination, but both areas may still be involved in the task. In this case, savings, but of a different magnitude, might be expected by both groups at R_1. A third possibility is that both areas are involved in an equal way. This outcome also predicts savings for both groups at R_1. Thus, comparison of the performance of these two groups at R_1, and R_2 with

each other, and with rats receiving asymmetrical successive bilateral or simultaneous bilateral lesions as in Experiment 2, will allow a further assessment of the generality of the effects of sequential damage to visual cortex independent of the position of the lesion.

METHOD

Subjects

The subjects were 34 male Long-Evans hooded rats, 90-120 days old at the beginning of the experiment. They were housed in individual cages with ad libidum food and water.

Apparatus and training

The apparatus and training procedures were the ones employed in Experiment 1 and they are fully described above.

In this experiment the stimuli were the ones employed in Experiment 2. The rats were run in squads of 6. Each squad included subjects from 3 or 4 groups.

Surgery and Histology

Surgery was performed according to the procedure described fully in Experiment 2. The extent of the visual cortex for the medial and lateral visual cortex was the same as the extent of the respective areas described in Experiment 2. The medial visual cortex included all of area 18 and the medial half of area 17. The lateral visual cortex included all of area 18a and the lateral half of area 17 (Krieg, 1946). The ML group received a first-stage lesion which included the medial part of the visual cortex bilaterally; the second-stage lesion for this group included the lateral part of the visual cortex bilaterally. The LM group received a first-stage lesion which included the lateral part of the visual cortex bilaterally; the second-stage lesion for this group included the medial

part of the visual cortex bilaterally. The SB group received a first-stage lesion which included the medial part of the visual cortex of the right hemisphere, and the lateral part of the visual cortex of the left hemisphere; the second-stage lesion for this group included the remaining visual cortex of each hemisphere. The bilateral group received a one-stage lesion involving all of areas 17, 18 and 18a bilaterally. Surgery was performed according to the schedule of Table 5.

Histological procedures were like those described in Experiment 1.

Procedure

The subjects were randomly assigned to four groups. The main experimental groups were: SB, N = 5; ML, N = 12; LM, N = 12; B, N = 5. Two subjects from the ML and the LM were randomly selected after R_1 and these animals did not receive a second lesion, so that the extent of the neocortical damage and lateral geniculate degeneration might be assessed following a partial bilateral lesion. Training and surgical procedures were similar to those described for Experiment 2. A summary of the experimental procedures is shown in Table 5.

Table 5

Schedule of Experimental Procedures

GROUPS	N	DAYS 1-6	7	17-18	19	29
B	5	A	-	R_1*	V	R_2
SB	5	A	vb	R_1*	vb	R_2
ML	12**	A	vm	R_1*	vl	R_2
LM	12**	A	vl	R_1	vm	R_2

*overtraining to a total of 50 trials

**Two animals from these groups were randomly selected after R_1 and these animals did not receive a second lesion, so that the extent of the neocortical damage and LGN degeneration might be assessed after the first stage lesion.

Abbreviations:
- A: Acquisition
- R_1: First retention test
- R_2: Second retention test
- V: Bilateral visual cortex lesion
- vb: partial bilateral visual cortex lesion
- vm: partial bilateral visual cortex lesion involving the medial visual cortex bilaterally
- vl: partial bilateral visual cortex lesion involving the lateral visual cortex bilaterally

RESULTS

Histological results are not yet available.

Behavioral

Table 6 presents the number of trials and errors required to reach 18/20 correct responses for acquisition, R_1 and R_2 for the four groups in the experiment. The results are also presented in the form of acquisition and retention functions in Figures 9 and 10. These functions were constructed in the same manner as the comparable functions described in Experiment 2. All statistical analyses were done using one-way analysis of variance and Newman-Keuls tests as in Experiment 2.

Figure 9 presents the acquisition functions for the four groups. For preoperative acquisition no significant differences were found among the groups for either trials ($F = 2.16$, $p > .05$) or errors ($F = 1.45$, $p > .05$).

Figure 9 also presents R_1 functions for the four groups. All groups reached criterion levels at R_1 with considerable savings over original learning. A t-test for dependent groups showed that the number of trials required to reach criterion at acquisition differed significantly from the number of trials at R_1 for all groups ($p < .001$). But even though all groups reached criterion at R_1 with considerable savings, an analysis of variance of savings scores at R_1 indicated significant differences among the groups for savings scores ($F = 4.05$, $p < .05$). Newman-Keuls comparisons showed a significant

Table 6

Mean trials and errors required to reach criterion for pre-operative acquisition, R_1 and R_2, as a function of the lesion employed. Savings scores for trials are included for R_1 and R_2 tests. The trial scores do not include the criterion block.

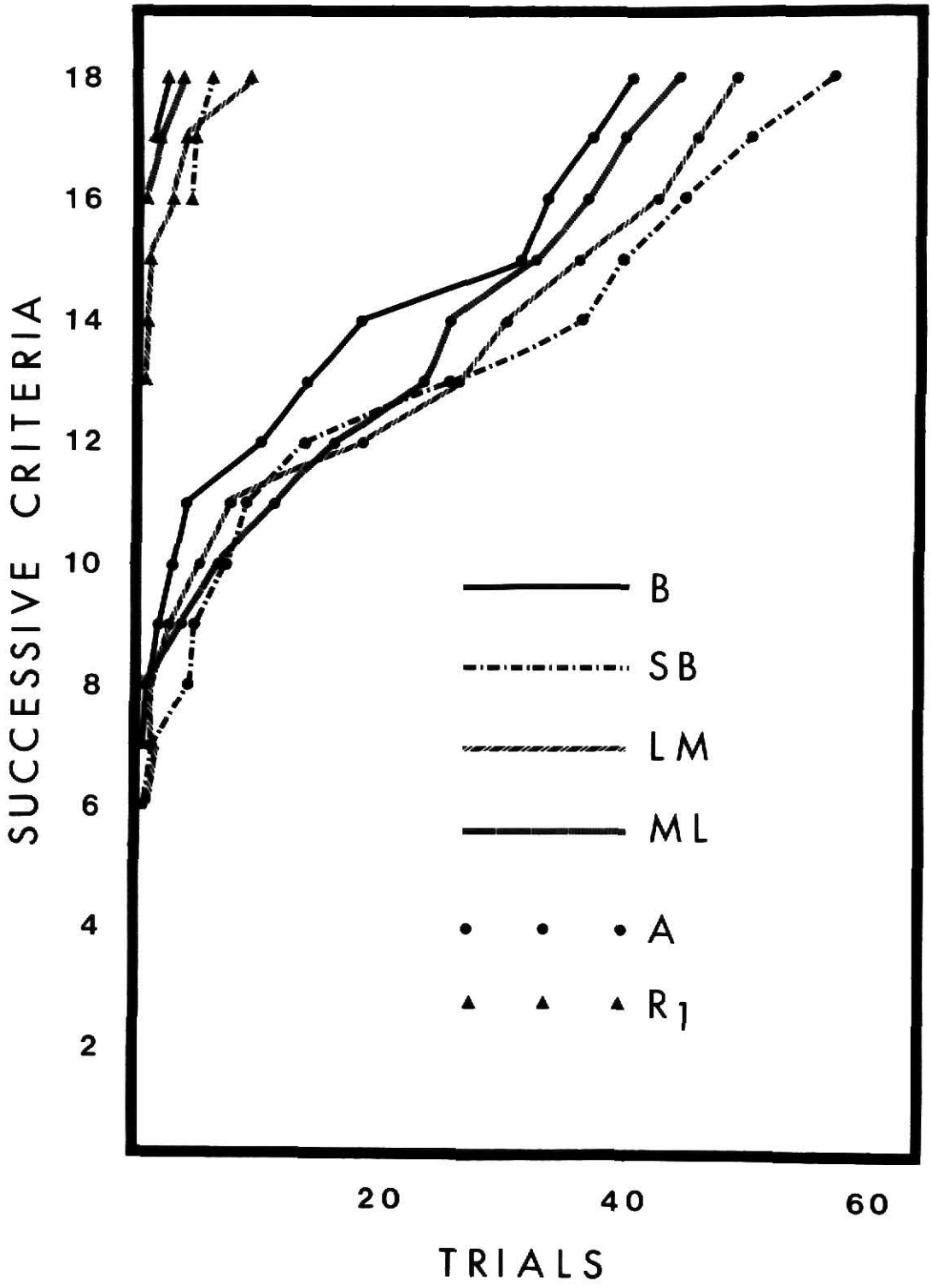
		Acquisition		Retention 1			Retention 2		
Group	N	T	E	T	E	%S(T)	T	E	%S(T)
B	5	40.2	20.2	2.2	0.6	91.0	46.8	18.2	-7.0
SB	5	56.6	26.8	6.0	2.2	83.6	17.8	6.8	60.6
ML	12*	44.3	21.9	2.3	0.9	92.0	8.3	3.3	68.4
LM	12*	46.3	27.9	10.3	3.6	68.2	4.9	2.3	80.8

*Two animals from this group were randomly selected after R_1 and these animals did not receive a second lesion, so that the extent of the neocortical damage and LGN degeneration following one-stage partial bilateral lesions might be assessed after the first-stage lesion. Therefore, only 10 subjects were included at R_2.

Savings scores were computed by subtracting the appropriate retention trials (R_1 and R_2) from the number of trials to acquisition (A), and dividing by the sum of the particular retention trials and trials to acquisition. The resulting saving scores were converted to percentages by multiplying by 100: (A-Ri/A+Ri)(100).

Figure Caption

Figure 9. Original acquisition and R_1 functions for the 4 experimental groups. 1 through 18 successive criteria are along the ordinate; number of trials required to reach each of the successive criteria is along the abscissa. See text for explanation of the computation of each point on the curve.


SUCCESSIVE CRITERIA
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LM
ML
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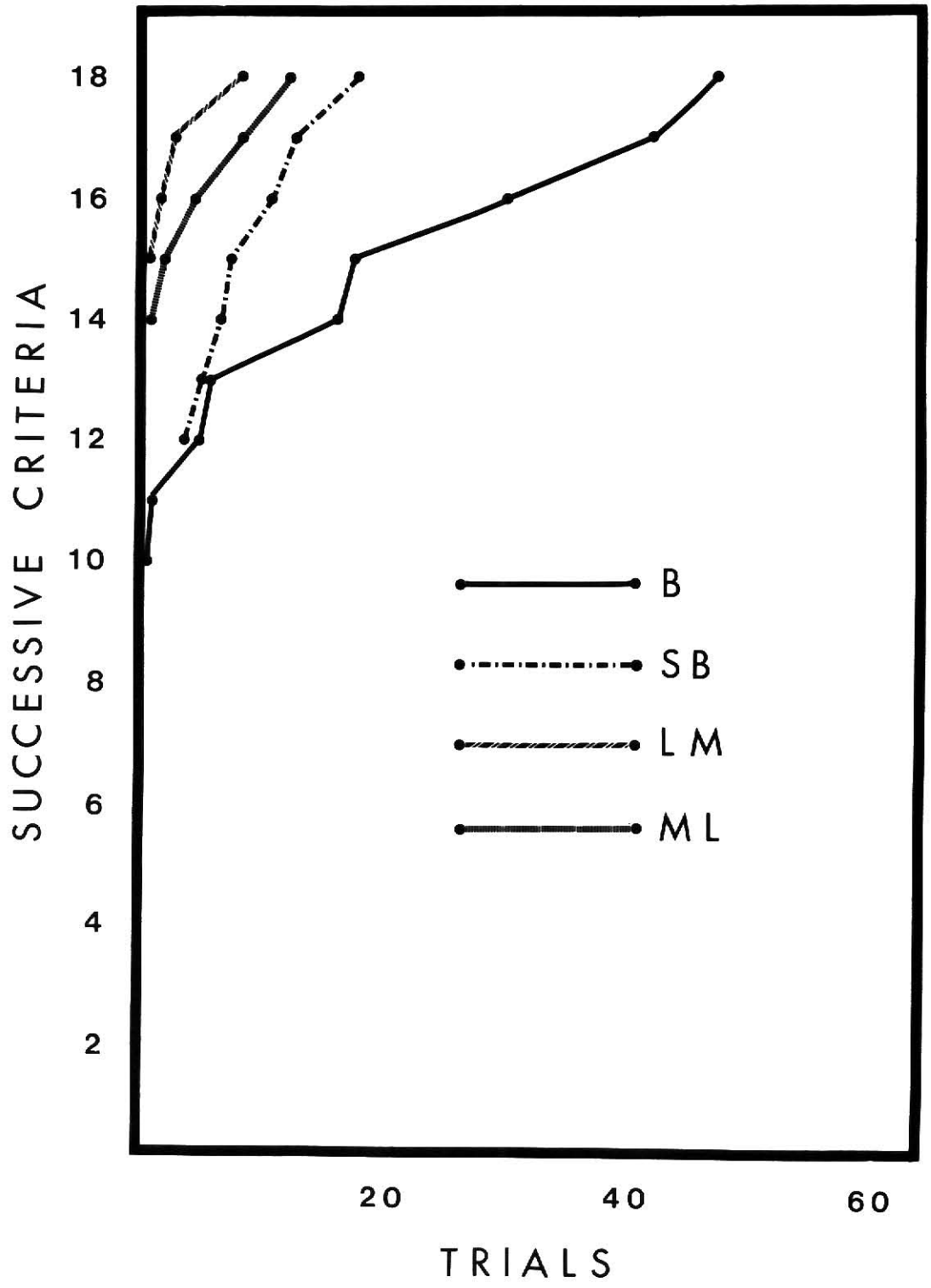
R1

Figure Caption

Figure 10: R_2 functions for the 4 experimental groups. 1 through 18 successive criteria are along the ordinate; number of trials required to reach each of the successive criteria is along the abscissa. See text for explanation of the computation of each point on the curve.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difference between the ML and the LM group ($p < .05$). No other pair comparisons reached significance. Table 6 indicates that the LM group required more trials to reach criterion than any of the other groups. It thus appears that damage to the lateral portion of the visual cortex results in a slight retention deficit.

Figure 10 presents R_2 functions for the four groups. Significant differences among the groups were found for savings scores ($F = 16.43$, $p < .01$). Newman-Keuls comparisons showed no significant differences between any pairs comparing successive lesion groups. However, all three successive lesion groups differed significantly from the bilateral group in savings scores ($p < .01$).

All successive groups reached R_2 criteria with considerable savings. A t-test for dependent groups showed that R_2 criteria were reached in considerably less trials than the number of trials required for preoperative acquisition in all three successive groups ($p < .001$). The B group showed a loss of the habit at R_2. No significant differences were found between acquisition trials to criterion and R_2 trials to criterion for the B group. It is concluded that the successive groups reach R_2 criteria with savings, whereas the B group shows a loss of the black-white task.

DISCUSSION

The present experiment found that all groups reached preoperative criteria with considerable savings at R_1. The LM group showed a slight retention deficit at R_1, but these animals still reached criterion with considerable savings. These data suggest that neither medial nor lateral portions of the visual cortex are critical for the brightness discrimination. This result is consistent with Lashley's (1931) findings which first demonstrated that no part of the visual cortex was critical for the acquisition or relearning of black-white habits, but that the lateral visual cortex may play a more important role nevertheless. The conclusion that the lateral visual cortex is not alone responsible for the discrimination is further demonstrated by the R_2 findings of the ML group. This group received a medial visual cortex lesion during the first stage of the ablation, followed by bilateral ablation of the lateral visual cortex during the second stage of the ablation. If the medial visual cortex was irrelevant to the task, subsequent ablation of the lateral, and presumably relevant visual cortex, would result in a loss of the habit for this group. However, these subjects showed considerable savings at R_2.

The results of the present experiment with subjects receiving simultaneous bilateral (group B) or asymmetrical successive bilateral (SB) visual cortex lesions replicated

those of Experiment 2. In addition, rats receiving sequential bilateral visual cortex lesions involving first the lateral aspects of each visual cortex bilaterally, and then the medial aspects (group LM), or first the medial and then the lateral aspects (group ML) all showed savings of the black-white discrimination at R_2. Combined scores for R_1 and R_2 were less for the successive than for the bilateral subjects. Thus it appears that it is not a matter of substituting R_1 for R_2 training,but rather it appears that the successive subjects relearn with savings whereas the bilateral subjects show a loss of the habit. Thus the present results indicate that partial damage to the visual cortex in general, including a variety of both unilateral and bilateral loci, produces a facilitation of recovery from final total damage of that region of the brain. The results with the various successive bilateral lesions are consistent with the Finger et al (1971) data where the successive bilateral effect was first demonstrated in the somatosensory system. The present data extend Finger's (1971) findings to the visual system when a variety of successive bilateral lesions are made on the visual cortex of rats.

The mechanisms by which partial successive brain damage can facilitate or enhance behavioral recovery from eventual total damage to a brain region are unknown. However, several possibilities may be considered which are consistent with the present results. Relearning of a black-white discrimination habit following posterior decortication indicates than an

extrastriate mechanism can support the habit. The successive lesion effect could be due to an active reorganization of an extrastriate mechanism after the partial lesion (Stein et al, 1969). Or it could be due to an active suppression by the posterior neocortex on an extrastriate mechanism with a partial release phenomenon after the partial lesion (Glendenning, 1972). Orthogonal to these alternatives, the second or extrastriate mechanism could be involved in original learning (Braun et al, 1966; LeVere and Morlock, 1973), or it could come into play only after damage, with partial damage bringing it in a little at a time. The present data are consistent with, but do not differentiate between the above alternatives.

The extrastriate mechanism involved in the recovery could be either cortical or subcortical. Earlier investigators (Lashley, 1931; Horel et al, 1966) have hypothesized that the extrastriate visual mechanism involved in the discrimination is subcortical. This is feasible in view of the fact that the entire posterior neocortex has been typically ablated in the past. Moreover, Lashley (1931) and Horel et al (1966) have demonstrated relearning of a black-white habit following total decortication in the rat. In the present study an attempt was made to confine the lesion to the visual cortex as was electrophysiologically defined by Montero (1973); Montero et al (1973); Adams and Forrester (1968). Therefore, it is possible that extrastriate posterior cortical areas may be also involved in the recovery in the present case. Due to the nature of the present lesion, these experiments cannot

conclusively state the site of recovery. Further experimentation using this smaller lesion is needed to answer this question. The present data do, however, demonstrate that the small, precise lesion used in the present studies produces the same effects as were demonstrated in the past with larger lesions (Thompson, 1960; Horel et al, 1966).

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EFFECTS OF SEQUENTIAL LESIONS OF THE VISUAL CORTEX ON RELEARNING OF PATTERN OR BRIGHTNESS DISCRIMINATIONS IN THE RAT

by

HELEN BARBAS

B.A., Newark State College, 1972

AN ABSTRACT OF A MASTER'S THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Psychology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1974

ABSTRACT

The effects of sequential lesions to the visual cortex of rats on the relearning of pattern and black-white discrimination tasks were assessed.

Rats subjected to either two-stage lesions or to one-stage visual cortex lesions were compared on a two-choice pattern discrimination task in which total luminous flux, systematic local flux and contour cues were absent. The performance of rats with two-stage visual cortex lesions was superior to that of rats with one-stage bilateral lesions. Nine out of ten serially lesioned rats reached criterion, but none of the bilateral subjects relearned within 550 trials. Two out of four bilateral subjects trained to 850 trials relearned the discrimination. It is concluded that sequential damage to the visual cortex facilitates relearning of a pattern discrimination task. Bilaterally lesioned rats were also able to relearn the pattern discrimination when extensive training was given.

The purpose of the black-white studies was to demonstrate whether the sequential lesion facilitation effect is a general phenomenon. This was accomplished by employing a variery of successive bilateral lesions. Sparing of a black-white discrimination habit in rats subjected to successive visual cortex lesions was independent of the nature or locus of the lesion. Serially lesioned rats with successive unilateral or various successive bilateral lesions relearned the discrimination

with savings, but one-stage bilateral subjects were retarded in reaching preoperative criteria. These results demonstrate the generality of serial damage to the visual cortex in sparing the preoperatively learned discrimination, as contrasted with the severe deficits resulting from one-stage bilateral ablation of the visual cortex.