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Cortical and Subcortical Interhemispheric Interrelation in the Visual System

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CORTICAL AND SUBCORTICAL
INTERHEMISPHERIC INTERRELATION
IN THE VISUAL SYSTEM

by

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George C. Wagner

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INTRODUCTION

Equivalence of learning and relearning mechanisms:

In an effort to locate the brain structures wherein a discrimination task is learned and stored as memory, Lashley explored the visual system of the hooded rat. He systematically varied lesion sites, training time (pre- or postoperative) and visual cues while testing subjects in the jumping stand or Yerkes apparatus (Lashley, 1930).

His major finding was that both pattern and brightness discriminations are not retained after bilateral posterior cortex lesions and only a brightness discrimination can be relearned (Lashley, 1922, 1933). Lashley noted with some interest that the relearning of the brightness discrimination required the same number of trials as the original preoperative learning (Lashley, 1933, 1935). The importance of this latter finding was that it suggested to explore the possible equivalence of the original learning and postoperative relearning mechanisms.

Lashley's discussion of diaschisis (a theory stating that a disturbance to one part of the CNS may alter the function of some other part) suggested that the relearning mechanism was isocortical (Lashley, 1922, 1935). With empirical exploration, however, he concluded

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that the anterior cortex is not involved in the brightness discrimination task (Lashley, 1933, 1935). The obvious alternative was that the subcortex is involved in at least the relearning. It should be noted here that the same phenomenon occurs when a reflected brightness discrimination is used in place of the Yerkes emitted brightness discrimination. Thus, rats relearn a black versus white cue card discrimination in the same number of trials as they learned it in before visual cortical destruction and regardless of whether or not the anterior cortex is intact (Meyer, 1971; Horel, Bettinger, Royce and Meyer, 1966). Still the question of the possible equivalence of the two mechanisms was not solved.

In an experiment dealing directly with this, Lashley changed the task slightly by requiring the rat to discriminate between two different intensities as opposed to simply choosing the alley with the light on during any trial (Lashley, 1933, 1935). The new task is obviously more difficult and, as expected, the subjects with visual cortical destruction took longer to relearn the task than their preoperative performance. Although the task was modified slightly, results were provocative.

There is now evidence that learning a black-white discrimination after posterior cortex destruction does

not proceed at the same rate as the original learning. Apparently Lashley's results were the fortuitous result of comparing only the total number of trials to criterion. Horel et al. (1966) plotted successive criteria curves and found that normal subjects exhibited an aversion towards the white cue card in the early stages of learning. This bias had to be overcome before learning could occur. However, decorticate subjects, on relearning the task responded with equal probability to both cards in the first trials. Thus, they did not show this white card bias, a point which caused Horel et al. (1966) to postulate the nonequivalence of the two systems.

Spear and Braun (1969) noted that the Horel et al. successive criteria graphs converged at a point near the highest criteria used (nine correct responses out of ten). They suggest that if Horel et al. had extended their study to more stringent criteria or manipulated the degree of aversion of the positive cue that the functions of the two groups, normals and decorticate, would cross and diverge.

They replicated the Horel et al. study manipulating the intensity of the positive cue (high intensity = high aversion for normals) and criteria difficulty. Their conclusions were that decorticate subjects reached lower criteria in fewer trials than normals but were retarded in reaching more stringent criteria with low

aversion positive cues.

From the above studies the general conclusions were that there are distinct mechansisms involved in the learning and relearning of the discrimination. The most likley place for this second visual system is the subcortical projection areas, since the studies of Lashley and Meyer have indicated the anterior cortex to be without importance in relearning.

The relevant cue: CNS interpretation:

Bauer and Cooper (1964) and Cooper, Blochert, Gillespie and Miller (1972) found that rats, if trained on a brightness discrimination while wearing translucent contact lenses, showed signs of partial retention after visual decortication. They suggested that the eye lenses forced the subjects to utilize flux cues, which survived the cortical lesion, presumably within the subcortical visual system. This would mean that a normal subject, without lenses, would learn a brightness discrimination task on cues other than flux, and it is these cues which are lost after decortication. Lashley did a similar study yielding results supportive of the above conclusions. He trained rats on a brightness discrimination task and then removed their natural lenses, destroying pattern vision edge cues. There was no retention of the task although no brain extirpation was performed and although the subjects could relearn the

discrimination (Lashley, 1937). It thus appears that the cortex, if intact and receiving detail information, is functional in brightness discrimination. If, however, the detail edge cues are not available, the subcortex is brought into play and the discrimination is learned on the basis of flux information.

The above interpretation is subject to question. Braun, Meyer and Meyer (1966) trained rats in a standard black-white task and performed bilateral posterior cortical lesions. Prior to relearning they injected amphetamine systemically and found a partial reinstatement of the habit as evidenced by savings scores. Since the amphetamine had no effect on the learning by naive subjects, Braun et al. concluded that the amphetamine facilitated access to flux engrams formed in the subcortex during initial learning.

Electrophysiological data may resolve the issue to some extent. Hubel and Weisel (1962, 1959) have categorized cortical cells as having either of two receptive fields, simple or complex. Complex cells respond only to specifically oriented edges of light analogous to detail or pattern cues. Simple cells, on the other hand, respond to a more diffuse stimulus similiar to the brightness discrimination task cues. Complex and simple cells are found in the visual cortex yet only simple cells have been found in the subcortical visual system (eg. superior colliculus).

Serial Ablation:

An interesting variation of bilateral decortication is to operate on one hemisphere at a time. The interim phase between the two operations, provides the opportunity to introduce several variables.

Meyer, Isaac and Maher (1958) investigated the effects of sequential lesions on the spontaneous reorganization of a visually cued, shuttle box avoidance task. They found that bilateral posterior decortication led to loss of the habit. Also, serial ablations, performed within six days of each other, led to a temporary loss of the habit. However, serial lesions performed twelve days apart, with subjects houled in their home cage, did not affect avoidance performance.

This finding was quickly applied to a more conventional discrimination situation. Thompson (1960) trained subjects in a black-white situation and performed serial ablations on the anterior or the posterior cortex. He also varied the twelve day interoperative phase by giving retention tests to some of the subjects. He found that after recovery from the second operation, subjects with only anterior lesions had no deficit. Also, subjects with interoperative retention training almost completely retained the discrimination after the second operation. Subjects without interoperative training had a deficit in relearning the task but this

deficit was not as severe as the one exhibited by the
simultaneous operative group.

Glendenning (unpublished dissertation) confirmed
and extended these results. He manipulated interoperative
training and eye occlusion in addition to serial lesions.
With the eye occluders, Glendenning was able to restrict
visual input, to a great extent, and thus force a
subject to use his good, unlesioned side or his deficient,
subcortical side in the interoperative retraining. The
important addition of the study was that a subject forced
interoperatively to relearn a task utilizing only the
eye with most of it's fiber projection to the subcortex
did not fully retain the discrimination after the second
ablation. Thus, the occluded visual cortex still had
an effect during relearning.

In the latest of the serial ablation studies
Seitz extended the interoperative phase variables to
include a roughness discrimination task. His results
indicate that nearly any form of interoperative training
will suffice to reinstate the visual habit, or increase
savings scores (Seitz, unpublished thesis, 1972).

Glendenning and Seitz concluded that there is a
dominance suppressive interaction between the subcortex
and the cortex in the visual system. The unilateral
occluded cortex actively suppressed the subcortex's
relearning of the habit, as evidenced by the partial
loss of the habit following its removal.

Unilateral Lesions:

Closely related to the serial ablation manipulation is a recent series of studies. These involve operating only on one hemisphere and training. Boles (1969) reported that rats with unilateral visual destruction are enhanced learners of visual pattern discrimination. Levension, Hottaman and Sheridan (1971) extended the research in this area when they enucleated the eye of a subject (pseudolesion) in addition to studying the enhancement effect on black-white discriminations. In essence, they found no enhancement after enucleation and no enhancement in the black-white discrimination.

The theory presented is that there is a release of interhemispheric inhibition with unilateral destruction. Thus, this series of studies directed attention away from the intrahemispheric interaction.

Interhemispheric Interaction:

It was originally theorized that the coexistence of symmetrical hemispheres is complementary with each brain structure keeping its counterpart informed via an inter-structural commissural system. This was referred to by Sperry as the carbon copy theory of engram transfer (Sperry, 1961). The typical experiment entailed a cat with a split corpus callosum and transected optic chaism, leaving each eye project to the ipsilateral hemisphere

(Sperry, 1961; Myers, 1955). The ensuing research dealt with which tasks learned monocularly could be performed by the contralateral hemisphere.

In a study by Meikle and Sechzer (1960) it was found that although visual pattern discrimination did not transfer in split brain cats, simple brightness tasks did. Their experiment involved the occlusion of one eye while the other was being trained. Yet they found transfer of a learned response to the other hemisphere without a corpus callosum. It was suggested that the brightness discrimination task had a subcallosal pathway which was used to transfer the engram to the other side.

In another experiment Sechzer (1964) repeated the earlier procedures using a shock avoidance motivating force, as opposed to food reinforcement. Surprisingly, she found near complete transfer of pattern tasks in split brain cats. In the second part of this experiment she repeated the study using food reward and found no transfer. She postulated that the transfer was due to subcallosal visual pathways that come into play only during shock avoidance motivation.

Sprague added another dimension to the inter-hemispheric notion. Using cats, he ablated the cortex of one hemisphere. This produced a deficit in orientation in the corresponding field of vision. Upon ablating the contralateral superior colliculus there

was a complete reinstatement of the orientation response.
A superior collicular commissurectomy had a similiar
effect although a recovery period was necessary.
Sprague concluaed that there was intercollicular
inhibition released only after the second lession
(Sprague, 1963).

In a follow-up study, an attempt was made to investi-
gate this phenomenon in a discrimination paradigm.
Wagner and Kratz (unpublished data) postulated that the
release of inhibition may result in enhancement of
learning of a brightness discrimination and possible
pattern discrimination after bilateral posterior
destruction. Neither result was fulfilled.

Greenfield and Meyer (unpublished undergraduate
thesis) extended Sprague's findings to the rat species
and using hooded rats found that it is collicular
inhibition and not cortical-collicular inhibition.

This study is designed to investigate further,
the nature of these proposed inhibitory forces. With
combinations of eye occlusions and serial and unilateral
lesions, the nature of the inhibitory mechanism can
be reviewed.

The theoretical contention here is that the sub-
cortex, in an intact subject, functions during learning
tasks. The term inhibition and the postulated dominance-
suppression interaction between cortex and subcortex
are regarded as too general. The conflicting inter-

pretations cited above are believed due to species and procedure differences.

During preoperative phases of a learning experiment the subject is apparently utilizing his visual cortex. It's removal, as in the early Lashley studies, leads to zero retention. However, Cooper et al. studies using lenses, and the Braun et al. amphetamine experiments indicate the subcortex is functioning. Detail edge cues may be the crucial stimulus even in the black-white discrimination task. The subcortex is not able to assimilate this type of information, possibly because there are no complex cells. This would mean that the complex cells of the cortex are brought into play whenever available to the subject. The reason for this might be that the complex cells are in contact with and affected by a greater number of other cells. More stimulus data would be available to the subject if this were the case. Destruction of the complex cells after cortex lesions leave little or no information left to the subject, suggesting that the cortex dominated the subcortex. The Glendenning data can be interpretated along these lines also. His postulate was that the opposite cortex, after a unilateral lesion, is inhibiting the subcortex side, which the subject was forced to use. Lund, however, pointed out that hooded rats could use their opposite cortex due to an incomplete chaism decussation. Thus, complex cells were available to the unoccluded

eye which was supposedly utilizing only the subcortex after the unilateral cortex lesion. After the second unilateral cortex lesion these complex cells were no longer available to the subject and the retention score was very poor.

The Cooper et al. lens study and the Lashley eye lens removal study emphasize this. Complex cells, when used are learning edge cues. When edge cues are no longer available the subject can not use the complex cell information. The subject thus is forced to relearn the task on the basis of flux cue information. Here the subcortex can be brought into play since the flux cue information can be assimilated by the simple cells. And Cooper et al. were able to demonstrate excellant retention scores. Thus, when complex cells are not available to the subject or when detail edge cues are not detectable, flux cues are utilized.

The problem of the incomplete decussation in the hooded rat may be overcome by using Sprague-Dawley albino rats. Each eye projects to the contralateral hemisphere and no detail edge cues cross remaining commissures. Therefore, after a unilateral cortex lesion, the subject forced to use the contralateral eye, would learn black-white discriminations on the basis of flux information. This, according to the above theory, should be detectable by a high retention score after the second unilateral lesion.

If the data prove otherwise there would be three possible explanations. First, the opposite visual cortex, or the complex cells in the cortex, have been able to detect visual edge cues via the remaining commisural system and the subsequent destruction destroys any information available to the subject. Second, the opposite cortex in some manner managed to inhibit flux cues learned by the contralateral subcortex. But this inhibition took place only after its' removal or destruction. Third, the subcortex was able to learn the discrimination on the basis of detail edge cues which it was able to assimilate only when the contralateral cortex is intact.

METHODS

Subjects:

26 male, Sprague-Dawley rats divided into seven squads were successively obtained from the Upjohn[1] research labratories. Each squad consisted of four subjects, approximately 50 days old and weighing 185-205 grams. As one squad completed the experiment the next would be ordered, a procedure assuring symmetry amoung subjects. The death of two subjects in the first six squads was accounted for by the seventh squad of only two subjects.

All subjects were housed in individual cages with ad lib. access to food and water for the first week after arrival. They were handled for 10 minutes on each of the last three days of the first week after which the formal experiment (day 1) started. Experimental subjects were randomly designated to one of four groups and appropriate subjects were food deprived to 75% of the control subjects (squad 1) who were the same age as the experimental subjects but had ad lib. access to food and water throughout the experiment. Weight was taken every other day, and the amount of food alloted to each subject was adjusted. On experimental days subjects were not fed until between one and three hours after training.

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Apparatus:

A modified Thompson box was used. It was a replica
of the one described by Thompson and Bryant (1955)
Fig. 1, except it was set up for positive reinforcement
rather than shock avoidance as the motivating force.
The grid floor was replaced by standard 24 guage wire
mesh, tautly suspended above a table covered with cage
paper. The goal box was separated into two compartments.
Food cups were cylindrical, 11 cm in circumfrence and
.7 cm deep. The apparatus was constructed of 3/4 inch
pine and 1/8 inch plywood. Everything, including the
walls in the room was painted flat black unless other-
wise noted. The only source of illumination was a
100 watt bulb suspended over the start box door. Six
pairs of stimulus doors were used. All were 14 x 18 cm
and constructed of grey cardboard. Five pairs were
covered with contact paper, one black and one white,
and the sixth pair served as neutral grey doors. The
contact paper doors could be washed easily, a procedure
necessary for the control of olfactory cues.

The positive cue was always the white door behind
which was a white food cup. These were alternated
randomly between compartments according to a predeter-
mined schedule. The only contingency in the schedule
was that no more than three successive trials were to
the same side. The appropriate response was to push

Figure 1

A modified Thompson box, with dimensions in centimeters, used in this study. The light was 60 cm above the start box.
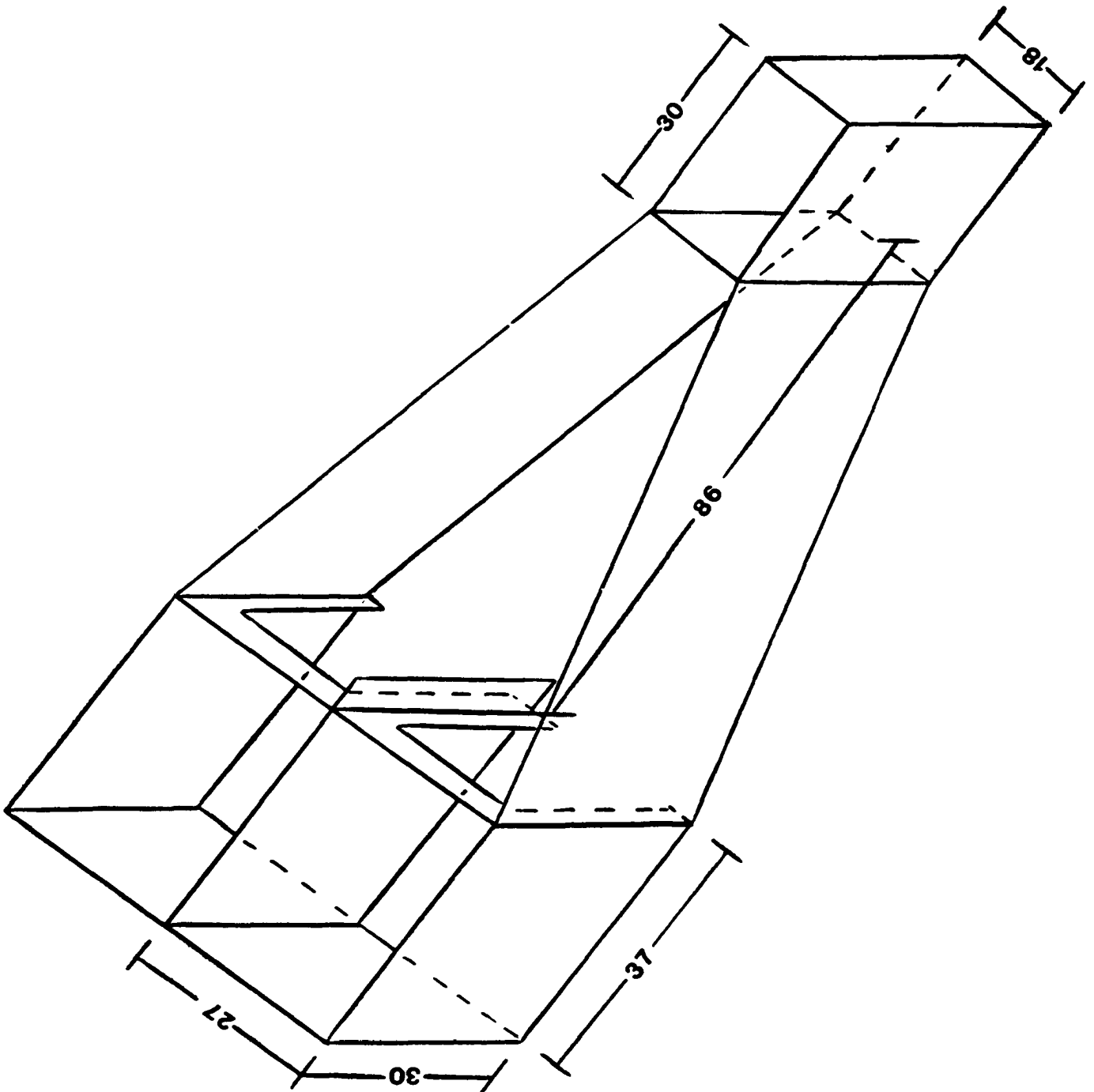
over the proper door. A noncorrection procedure was used.

Surgery:

All surgery was carried out under clean but not aseptic conditions using sodium pentobarbital anesthetic, 40/mg./kg. intraperitoneal. Atropine, .1cc was also given as a vagolytic agent.

After the anesthetic took effect the subjects heads were shaved and fixed into a sterotaxic instrument. Scalp tissue was incised and reflected with underlying periostium retracted to expose skull surface. Access to the visual cortex was gained by removal of the overlying skull between coronal and parietal sutures and from the sagittal sinus laterally to the rhinal fissure. A small isthmus, about 1mm wide, was left covering the sagittal sinus after bilateral craniotomy.

The dura and pia matter were then retracted laterally and the cortical grey aspirated. When possible the dura was replaced and Gelfoam was packed into the wound. Eye lids of appropiate subjects were sutured shut and the eye was covered with opthalamic ointment to guard against infection. The incision was sutured and the animal was returned to his home cage.

Procedure:

Pretraining was started when all subjects of the

squad were at the proper deprivation weight. This
consisted of a 15 minute adaptation to the apparatus
with the grey doors lying down (open) in the forward
part of the goal box chamber and the start box door was
closed. The subjects were placed in the alley and had
access to food in either chamber but were forced to
alternate since only limited amounts were available at
any one time in the food cup.

After the initial phase, above, subjects were
adapted to the start box for 45 seconds and then the
door was opened. When the subject moved into the alley
the door was lowered and the subject was allowed to
feed in one compartment for 15 seconds. Responses were
recorded and this was repeated three times.

The neutral grey doors were then stood up, ajar at
the center. If the subject wished to get to the food
it had to push the door over. This was repeated for
five trials; with each trial the grey doors were shut
further until the fifth when it was completely closed.
Food was behind either door but only one choice was
allowed. Responses were again recorded.

Finally, subjects were given ten trials of formal
black-white training. This was run the same way as the
former trials with upright doors, except the black and
white cue cards were used. The five pairs of cards were
washed and switched after each trial and the white
door alternated according to the previously mentioned

schedule. Incorrect responses (pushing over the black door) resulted in immediate replacement for 15 seconds plus the 45 second ITI.

On day 2, and until a criterion of 14 out of 15 correct responses was achieved, subjects were run 20 trials per day. Following criterion, subjects were rested for three days but were maintained on the 75% deprivation schedule. They were then retrained to criterion.

Groups:

	Stage I	Stage II	Stage III	Stage IV	Stage V
Group I	Normal	Ret.	Unilat. lesion	Ret.	Unilat. lesion
Group II	Normal	Ret.	Bilat. lesion		
Group III	Unilat. lesion	Ret.	Unilat. lesion		
Group IV	Unilat. lesion; Eye shut	Ret.	Unilat. lesion		

Each subject in squad was assigned to one of the above four groups. Group 1 and Group 2 rats were first trained to criterion. Group 1 was rested for three days while Group 2 subjects received sham operations, rested for three days and then all were retrained. After reaching criterion, the second time they were operated upon. Group 1 rats received unilateral lesions of the visual cortex and Group 2 rats received bilateral lesions of the same area. Following three days of recovery the

subjects were retrained to criterion, Group 2 subjects were then perfused while Group 1 rats rested three days, were retrained for retention, and then received contralateral cortical lesions, a recovery period and retraining before they were perfused.

Group 3 and Group 4 rats were operated upon before training, on day one. Group 3 subjects received unilateral lesions while Group 4 subjects received unilateral lesions plus ipsilateral eye suturing. On day four their training started and continued to criterion after which a three day retention test was given, similiar to the other groups. This was followed by contralateral lesions, recovery and relearning. They were also perfused upon completion.

Each group was to have five subjects at the completion of the experiment. Due to the death of two subjects in the first six squads, a seventh squad with two subjects was run. This completed Groups 3 and 4.

Surgery:

Figure 2 presents lesion reconstruction diagrams
for each of the 20 lesioned subjects. Lateral geniculate
degeneration was checked by cell counts after cresyl
violet stains of 50 micra sections of the frozen brain.
The lesions covered the target area well and were of
medium to large extent. Figure 3 is a representative
sample of histological photographs.

Training Results:

The trials to criterion scores of subjects in the
four groups over their respective treatments is presented
in Table 1. The Mann Whitney U test with a .05 alpha
level was the statistic used unless otherwise noted.

Group 1 and 2 subjects initially learned the task
as normals and their scores were combined as one group.
This combimed Group did not differ significantly from
the initial learning scores of the unilaterally lesioned
subjects of Group 3 ($P > .05$; $\bar{X} = 71$, $\bar{X} = 76$ for Group 1
and 3, respectively). They learned faster than the
unilateral lesioned, ipsilaterally occluded subjects
of Group 4 ($\bar{X} = 71$, $\bar{X} = 87$ respectively) but this
difference did not reach significance ($P < .08$).

For other statistical comparisons within and between

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Figure 2

Lashley diagrams for all subjects. Striped area indicates
cortical damage. Group numbers are at the bottom.

I   II   III   IV

Figure 3

Samples of histological photographs after bilateral
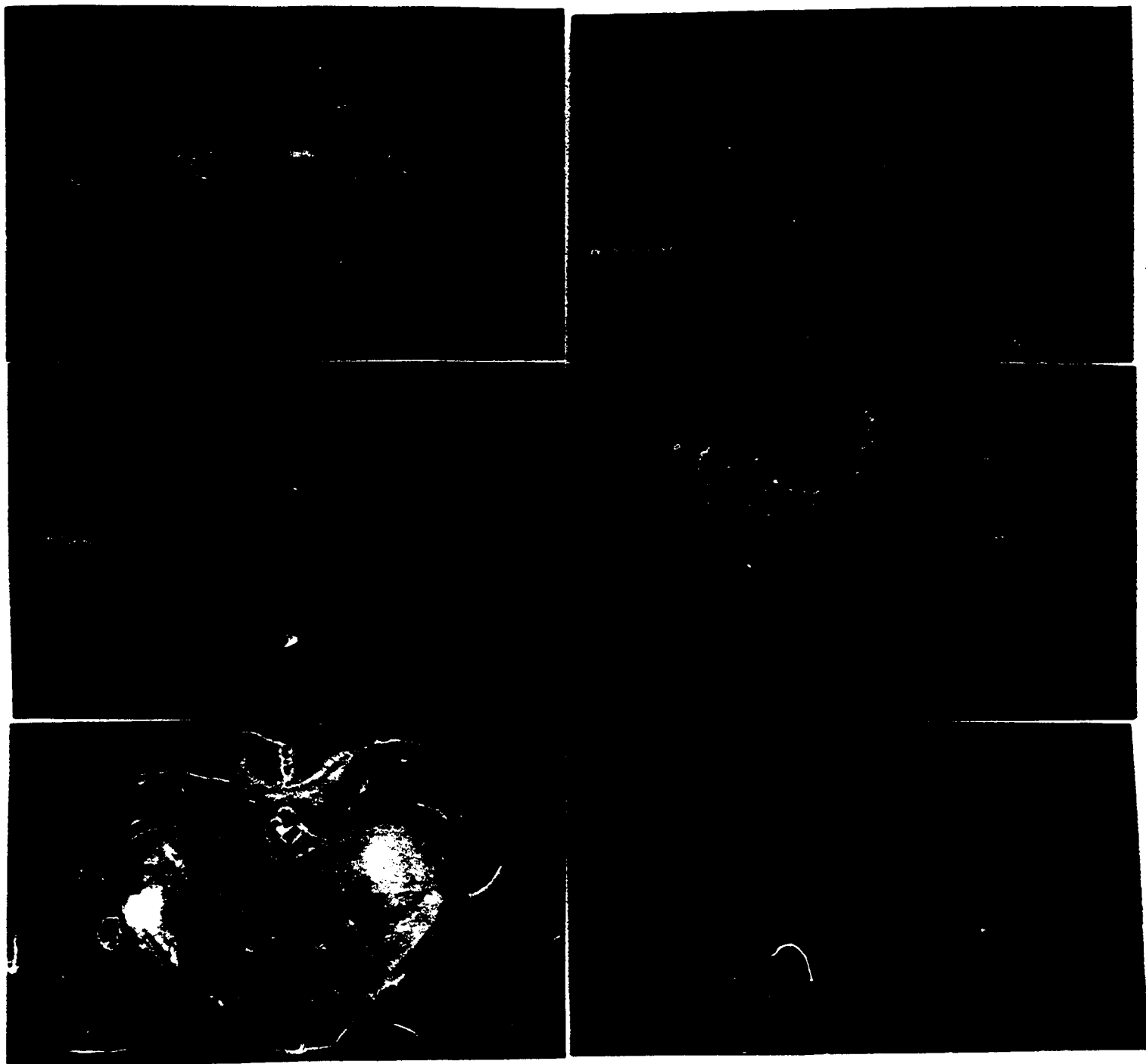destruction.

TABLE I

TRIALS TC CRITERION SCORES

S's		Normal	Retention	Unilateral lesion	Retention	Unilateral lesion
	1	48	14	19	19	30
	2	50	14	23	15	23
Group	3	94	17	60	20	74
I	4	90	16	40	15	22
	5	91	15	45	14	14

S's		Normal	Retention	Bilateral lesion
	1	77	15	60
	2	91	14	94
Group	3	72	15	80
II	4	65	14	79
	5	35	15	124

S's		Unilateral lesion	Retention	Unilateral lesion
	1	80	16	37
	2	105	15	32
Group	3	89	15	88
III	4	53	14	36
	5	55	15	17

S's		Unilateral eye shut	Retention	Unilateral lesion
	1	70	15	15
	2	108	19	27
Group	3	80	18	16
IV	4	118	30	35
	5	65	21	17

groups a retention score was developed to exclude some of the individual differences apparent in the initial learning trials to criterion scores. Individual differences are the primary source of within group variance and any statistically valid method of limiting it heightens the chances of between group differences becoming detectable. This was the reason for using this retention formula. Several hypothetical examples are presented below to clarify its use.

The basic formula is:

$$RS = (I - T)/ I$$

Where "RS" is the retention score acheived by a subject after completing a particular treatment or phase of the experiment in his group. "T" is the number of trials to criterion it took that subject to master that treatment (excluding the criterion trials). "I" is the number of trials to criterion for that subject's initial learning of the discrimination. Thus, "I" is the source of variance being eliminated.

If a subject initially learns the discrimination in 50 trials (I = 50), and during the second phase of the experiment had no errors (T = 0), his RS = 1 exhibiting perfect retention.

If a subject had a zero retention of the task in the second phase but relearned the task in 50 trials (T = 50), his RS = 0 exhibiting no retention.

If a subject had a deficit in relearning the task, for example needing 100 trials, (T = 100), his retention score has a negative valance; RS = -1. The retention scores for all subjects are presented in Table 2.

The normal subjects for Group 1 retained the task well after a three day lapse. The normal subjects of Group 2 received a sham lesion and also retained the task well after three days of recovery as did the subjects of Group 3 who learned with a unilateral lesion and had their retention test after a three day rest period. Group 4 exhibited a deficit in retention after their three day lapse. Their average retention score was .93 as opposed to .99 for Groups 1, 2, and 3. This difference was significant, (P < .05).

Group 2 subjects did not retain the discrimination after the bilateral lesion and averaged a zero retention score except for one subject who took nearly five times as many trials to relearn, with a retention score of -4.5. The difference in the learning and retention total number of trials was not significant (P > .05).

Unilateral lesions disrupted the memory of the learned task. Group 1 subjects had a mean retention score of .61 after the lesion but this was significantly better than the bilateralally lesioned subjects of group 2, but significantly worse than sham lesioned subjects or the normal subject retention scores of Groups 2 and 1 respectively, (P < .05).

TABLE II

RETENTION SCORES

	S's	Normal	Retention	Unilateral lesion	Retention	Unilateral lesion
	1	33	1.00	.88	.88	.55
	2	35	1.00	.82	1.00	.82
Group	3	79	.98	.43	.90	.25
I	4	75	1.00	.67	1.00	.90
	5	75	1.00	.60	1.00	.64

	S's	Normal	Retention	Bilateral lesion
	1	62	1.00	.27
	2	76	1.00	-.04
Group	3	67	1.00	.03
II	4	50	1.00	-.28
	5	20	1.00	-4.50

	S's	Unilateral lesion	Retention	Unilateral lesion
	1	65	.99	.66
	2	90	1.00	.92
Group	3	74	1.00	.01
III	4	38	1.00	.45
	5	40	1.00	.95

	S's	Unilateral eye shut	Retention	Unilateral lesion
	1	55	1.00	1.00
	2	93	.96	.87
Group	3	65	.96	1.00
IV	4	103	.85	.80
	5	40	.88	.99

The second unilateral lesion of Groups 1 and 3 also disrupted memory of the task. The subjects did not fully retain the discrimination as evidenced by mean retention scores of .64 and .60 respectively. Again, these scores were significantly better than the bilaterally lesioned subject's retention scores of Group 2 for both comparisions but were signifcantly worse than the sham lesioned or normal subject's retention scores of Groups 2 and 1 respectively, (P < .05).

The retention scores after the second unilateral operation on the unilateral lesioned, ipsilaterally occluded subjects of Group 4 were significantly better than the bilaterally lesioned subjects of Group 2 (P < .05), as well as the initial unilateral lesion retention scores of Group 1 (P < .05). In addition, they were better than the retention scores of Group 1 subjects after the second unilateral lesion, $\bar{X}$ = .93 for Group 4 versus $\bar{X}$ = .64 for Group 1 but this difference just missed significance (P < .06). Also, Group 4 subjects were better than Group 3 subjects after the second lesion, $\bar{X}$ = .93 and $\bar{X}$ = .60 respectively but this again approached but did not reach significance (P < .07).

Figure 4 is a plot of the successive criteria scores of the normals (Groups 1 and 2) and the unilateral subjects of Group 3. Figure 5 is a plot of the same scores for Groups 1 and 2, above, versus the unilateral, lesioned,

ipsilateral occluded subjects of Group 4 and the bilateral relearning scores of subjects in Group 2. In both of the latter Groups there is evidence of less aversion towards the white cue card exhibited by the lesioned subjects as compared to the normal subjects. As expected, the bilateral and unilateral lesioned, ipsilateral occluded subjects exhibited less aversion than the unilateral subjects of Group 3, shown in Figure 3.

Figure 4

Successive criteria graphs for unilateral lesioned subjects
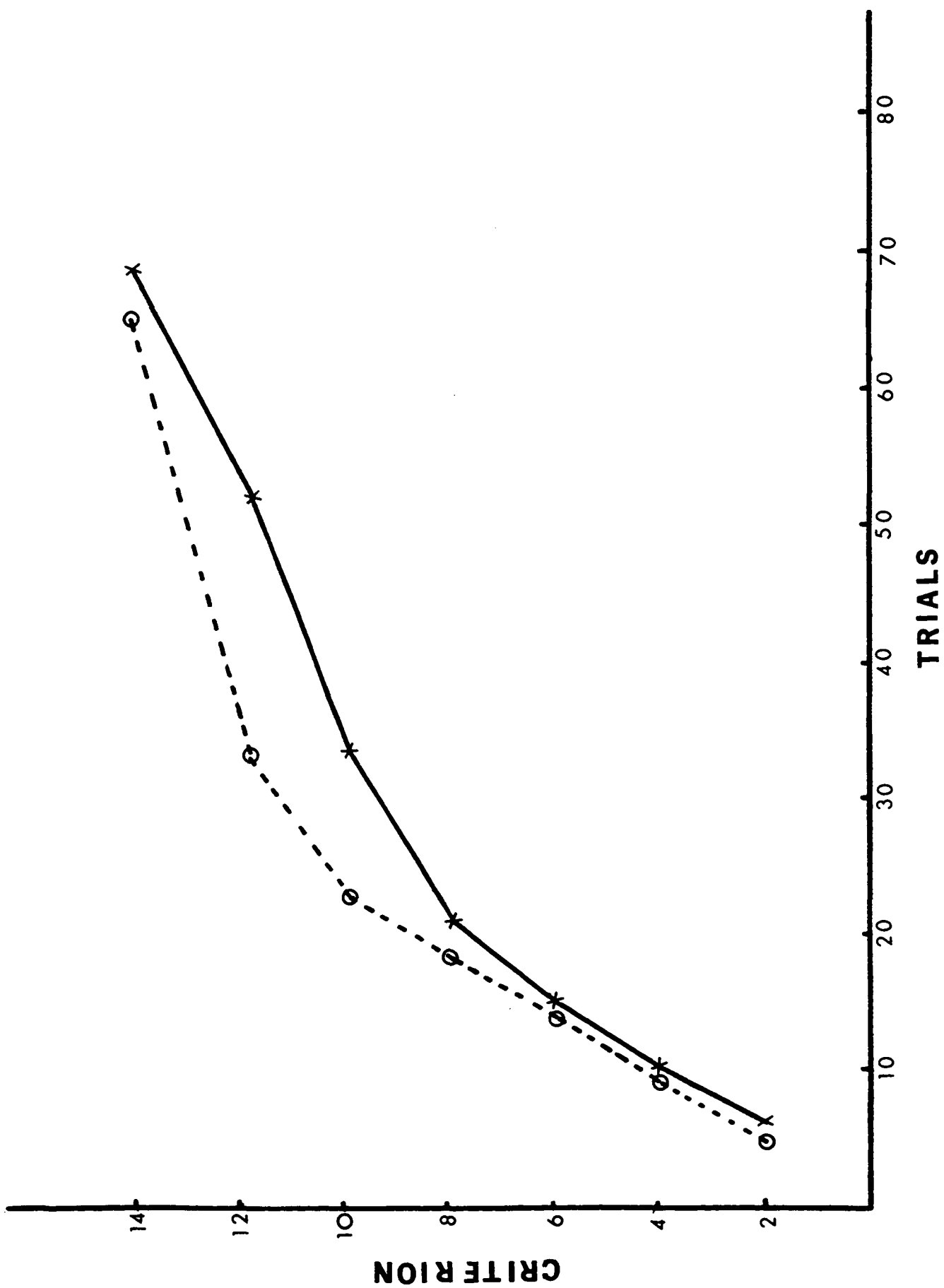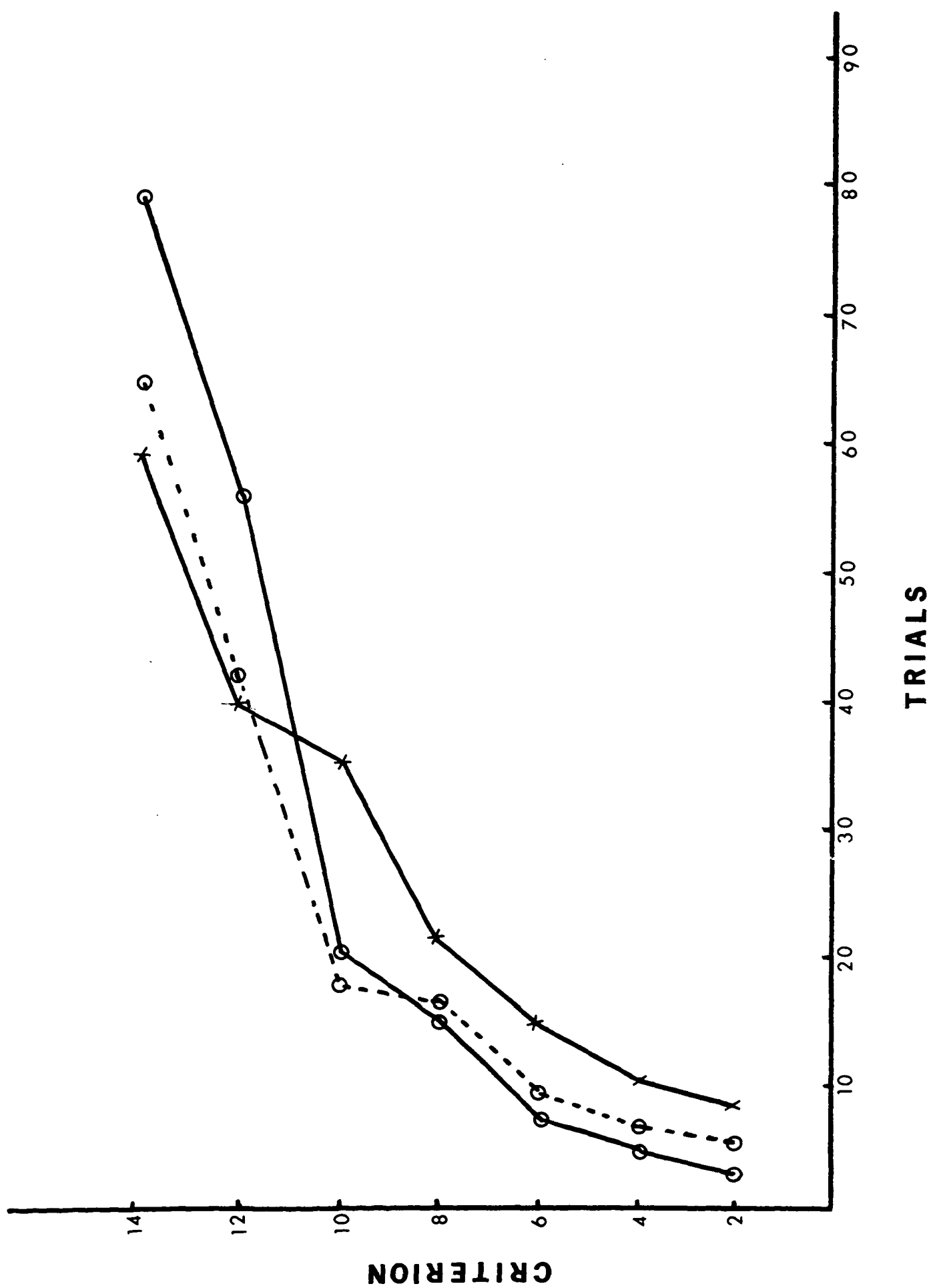o----o, versus normal subjects x----x.

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Figure 5

Successive criteria graphs for normals x——x, unilateral
lesioned, ipsilaterally occluded subjects o——o and
bilateral subjects o----o.

CRITERION

TRIALS

DISCUSSION

The results of this experiment are in accordance with several other studies. This is a noteworthy point considering that most Thompson box studies are run with shock as the motivating force while this experiment utilized food reinforcement.

First, Lashley's and Meyer's finding of a zero savings score after bilateral lesions was observed in Group 2. These results were translated into a zero retention score mean for four of the five subjects and a poorer score for the fifth subject.

Also, the partial retention score after serial ablations obtained in Groups 1 and 3 replicated the Thompson (1960) study. There was a variant in Group 3 subjects who received unilateral lesions prior to any training. The crucial training session apparently is the interoperative one. Whatever the mechanism utilized for this retention, it is not dependant upon training prior to the initial lesion.

The Boles and Sheridan finding that subjects with unilateral lesions are not enhanced learners of black-white discrimination was likewise confirmed by Group 3. This does not mean that the theory proposing a release of inhibition after unilateral lesions applies only to pattern discriminations. The failure to observe the

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enhancement phenomonon may be due to the fact that
initial learning for a black-white task proceeds at a
faster rate than a more difficult pattern discrimination.
This would mean that the effect would be less apparent
for a black-white task necessitating larger N or a more
stringent control of within group variance to observe
the effect.

Finally, the aversion towards the white cue card
in the early phases of training, which Horel et al. (1966)
noted, was also observed in Figures 3 and 4.

It is postulated that the unilateral lesioned,
ipsilateral occluded subjects of Group 4 learned the task
with their subcortex somewhat analogus to bilaterally
lesioned subjects. This assumption is based upon the
anatomical evidence of Lund (1965) and on the behavorial
evidence of Sheridan and Shrout (1966) which indicates
that input to one eye in the albino is nearly direct to
the contralateral hemisphere. It is supported by
evidence from this study of excellent retention of the
discrimination after the second unilateral cortical
lesion and by the fact that the subjects did not seem
to have an aversion towards the white cue card in the
early phase of learning, which is similiar to the
bilateral lesioned subjects and shown in Figure 4.

For convenience, this paper has referred to the
visual system as if it consisted of dichotomus aspects
of cortex and subcortex. One must be wary of any

intrepretations of data which are based upon this notion.
Theories have postulated that the cortex actively
inhibits the subcortex and that it is only after
lesioning that the subcortex is brought into play.
The amphetamine study of Braun et al. (1966) and the
translucent lens study of Cooper et al. (1972) have
shown the subcortex to be actively functioning. Further
evidence is supplied by Sterling and Wickelgren (1969)
and Wickelgren and Sterling (1969) who found complex
cells in the superior colliculus but showed them to be
cortically dependent. These data suggest a far more
complex relationship than a dominant suppressive one.
It is safer to regard the visual system as a unit with-
out reference to the encephalization suppression type
dicaotomy.

It has been postulated that complex cells are
utilized during pattern vision tasks while simple cells
are used during brightness discrimination. Also, if it
were true that complex cells have a frequency of response
that correlates with the intensity of the stimulus they
could be utilized for brightness discrimination as well.
The subsequent loss of brightness discrimination habits
after cortical extirpation could than be explained by
the destruction of the complex cells of the cortex.

Apparently the simple cells of the subcortex are
not dormant during the initial learning as evidenced by

the Braun et al. (1966) and Cooper et al. (1972) experiments. Meyer explained the results by saying the subject initially learns the task on the basis of detail information but must relearn the discrimination after these cues are no longer available. The above interpretation information available to the complex cells the simple cells can be utilized as effectively, thus explaining the Cooper et al. results.

It could be that the complex cells are the more efficient or, by virtue of a greater number of connections, called upon more often during learning. This theory is presented in the context of the present findings of excellent retention after the second unilateral lesion of Group 4 subjects. They orginally learned with one eye that projected to the subcortex unlike Glendenning's subjects who learned with one eye projecting to both the cortex and the subcortex. That projection to the cortex has been shown capable of supporting pattern vision (Sheridan and Shrout, 1966). Glendenning found deficits in retention after his second unilateral lesion which could be interpreted as resulting from destruction of complex cells of the cortex. This did not occur in the present study. The present theory accounts for this difference by postulating the complex cells of the intact cortex in Glendenning's rats were utilized for either of the above reasons. That is, complex cells, if available to the subject, are utilized and learn a black-white

discrimination on the basis of edge cues.

Concerning the interhemispheric relations between the two hemispheres there have been two major theories presented. Sperry suggests there is virtual independance between the two hemispheres and has been able to demonstrate simultaneous learning of discrete tasks. Boles and Sprague have suggested there is an inhibition between the two hemispheres.

The Sprague notion can be explained in a manner more congruous to the present interpretation of simple and complex cell activity. The unilateral lesion leaves complex cells intact and available to the eye being tested. These complex cells possibly override all other stimuli and regulate the attention to the stimuli in their own receptive fields. When the contralateral lesion or commisurectomy was placed this effectively isolated the contralateral subcortex allowing an independent function. Sprague's cats were thus functionally similiar to the rats in this study.

The enhancement of learning of a pattern discrimination poses a difficult question. It would seem the term inhibition is too general to rely upon as an explanation. The complex cells of the intact cortex may be utilizing information from both the ipsilateral and contralateral anterior cortex. If this were the case subjects with larger unilateral lesions including the anterior cortex as well as the posterior cortex would not show enhanced

learning. Sperry has shown this anterior cortex to be
involved in visual discriminations via indicating a
deficit after its removal. This once again suggests
that complex cells have ability to regulate the attention
of the subject. Schzer has also shown that with shock
as the motivating force discriminations can transfer.
Consequently an experiment run with food reinforcement
and pattern discrimination may not show the enhancement
effect.

The memory-performance distinction likewise poses
a problem of interpretation. Clearly the nature of
this study does not allow for a definitive statement.
Performance of a task can be affected by numerous
variables yielding a result unfortunately similiar to
memory loss. The consolidation experiments which utilize
electroconvulsive shock (eg. Duncan, 1949) induce what
appears to be short term memory loss. Performance
deficits are most easily noted when the motivating force
is not longer pertinent.

The theoretical framework of the experiment is
based on the assumption that memory is affected by the
brain extirpation and performance is not. Any performance
deficit would necessarily have to differentially affect
the different groups in this experiment. This type of
deficit can not be ruled out, however, since treatment
of the subjects also differed across groups.

[1] Upjohn Labratories, Kalamazoo, Michigan

[2] ibid

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