EFFECTS OF TRAINING ON RECOVERY OF
FUNCTION IN STRIATE RATS

by

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Acknowledgements

A number of years have been spent on research dealing with recovery of function following brain damage, particularly following cortical damage. Much of this research has been an attempt to clarify and expand the findings of Lashley (1935). He found that the ablation of the posterior (striate) neocortex of rats caused the loss of a previously learned brightness habit. He also found that it took these rats about the same number of trials to relearn the task as it did when the cortex was intact.

These results have led investigators in the field to pursue two lines of research. One line of research has been concerned with a functional comparison of the systems that replace the damaged cortex to the systems of the normal cortex. The other line of research has been concerned with the variables that speed up or enhance recovery from cortical damage.

Concerning the first line of research, it has been determined that the system taking over the damaged cortex's function does not function in the same way the damaged cortex does. This was concluded for several reasons. First, Horel, Bettenger, Royce, and Meyer (1966) demonstrated that while normal and striate animals take the same number of trials to learn a brightness discrimination this does not mean equivalence of the two systems. They plotted the learning curves of normal animals and animals without posterior cortex in a black-white, two-choice discrimination task in terms of the number of trials it took animals to reach successive criteria. The white door was defined as the positive cue; this was the positive cue that had been used in most black-white discrimination studies. They found that normal animals showed an aversion to the white door which the striate animals did not. The aversion to the white door temporarily slowed down the learning rate for the normal animals. Thus, the finding of equivalence in the number

of trials normal and striate animals take to learn the same task does not mean equivalence in the way they learn the task.

Second, evidence presented by Horel et al. (1966) suggested that the system that replaced the damaged cortex functioned subcortically. They found that the ablation of the entire cortex did not prevent an animal from learning a black-white discrimination. They also found that a posterior decorticate and a total decorticate were comparable in the number of trials required to learn the discrimination and in the general shapes of the successive criterion functions. If the replacement system for damaged posterior cortex functioned in the remaining undamaged cortex, it would be expected that removal of the entire cortex would slow down or eliminate learning of the discrimination. Since neither of these occurred, it could be concluded that the replacement system functioned subcortically.

Third, several experiments have shown that different cues have different affects on the two types of animals. Tsang (1937b) and Thompson (1970) found that striate animals could not discriminate patterns which normal animals could discriminate. Meyer, Treichler, and Meyer (1965) found that, when flux and contour were equated in two stimuli, striate animals could not discriminate between the stimuli but normal animals could. Mize, Thompson, and Wetzel (1971) found, however, that a striate animal could discriminate between patterns which were flux-equated provided that they differed greatly with respect to the total amount of edge or of contour they contained.

Bauer and Cooper (1964) and Hamilton and Treichler (1968) showed that normal animals use both available pattern and luminous flux cues to solve a black-white discrimination while striate rats use only luminous flux cues to

solve a black-white discrimination. They also found that increasing the light intensity of the stimuli made the task more difficult for the striate animals but not for the normal animals. Thus, it could be concluded from the above evidence that the system that replaces the damaged cortex is not equivalent in its ability to process information and that the replacement system functions subcortically.

The second major line of research has been concerned with what variables enhance recovery from cortical damage. One approach has been to damage the cortex of infant rats and then compare their deficits as adults with rats decorticated as adults. A second approach has been to determine what variables in the interval between two successive unilateral posterior cortical lesions enhance recovery of function. A third method has dealt with manipulations to improve recovery of function after bilateral posterior ablations given in adulthood.

One of the earliest approaches to the study of recovery of function was to damage the cortex of infant rats and then compare their adult performance with that of adult operated rats. Tsang (1937a) compared the behavior of rats with a variety of lesions given at twenty-seven days of age with the behavior of rats given the same lesions as adults. He found that even extensive cortical injury inflicted in infancy had less retarding effects on maze learning, in comparison with smaller lesions suffered in adulthood. He suggested that the infant rat brain was more pliable than the adult brain and this accounted for the difference found between infant and adult lesions.

Smith (1956) and Schwartz (1964) found that when they raised animals that had received cortical damage in infancy in an enriched environment (i.e. an environment that allowed the animals to practice perceptual and motor

skills), the decrement was less when compared to infant operated rats raised in their home cages.

Lesions given in infancy, however, result in the loss of pattern vision seen following adult posterior cortical ablations. Tsang (1937b), using a Lashley jumping stand, found that early lesions did not allow the adult animal to discriminate between two patterns. Bland and Cooper (1969) found that the combination of a visually rich environment and early lesions did not allow the animal to discriminate between two patterns at adulthood.

Thompson (1970) reviewed the findings of some of the infant ablation studies. He wanted to determine whether an animal that was operated on in infancy was more comparable to a normal rat or a rat that received the same ablation as an adult. When lesioned or normal rats were placed in an apparatus divided into two sections, light and dark, both of the operated groups preferred the lighted side while the normals preferred the dark side. Further, infant and adult operated animals could not learn a pattern discrimination which a normal animal could learn. However, all three groups of rats learned a black-white discrimination in the same number of trials. The only task in which the infant operated rat was more comparable to the normal rat than an adult operated rat was in an eight-cul maze. Both the normal and infant operated animals learned the task faster than the adult operated animals. Thompson concluded that the infant and adult operated rats were more comparable in their performance than the infant operated and normal rats. Thus, it appears that an operation in infancy allows a rat to recover some functions and not others. The amount of recovery is to some extent determined by the type of environment in which the animal is raised after the operation.

A second group of studies have tried to determine what variables in the interval between two successive posterior cortical lesions could alter recovery of function. Meyer, Issac, and Maher (1958) pretrained their animals in a shuttle-box avoidance task with light as the conditioned stimulus. After the pretraining, they operated and removed one side of the posterior cortex; they then waited twelve days and removed the other side of the posterior cortex. The animals either spent the interoperative period in their home cages or in a light proof chamber. Following the second operation animals were retrained. Sparing of the habit upon retraining was found in the group that was maintained in the home cages interoperatively, but the group that was maintained in the dark showed no sparing of the habit. There were two arguments that could have explained these findings. One argument would maintain that the general stimulation received by the rats in their home cages facilitated recovery. The other argument would maintain that the rats had a chance to practice the response in their cages and that this caused the recovery.

Issac (1964) replicated the Meyer, Issac, and Maher (1958) study with the use of several additional interoperative environments. He ran groups that received interoperative environments of light only, white noise only, light and white noise, and no light and white noise. He found that saving scores increased with the total amount of stimulation the animals received interoperatively. This indicated that interoperative practice was not the determinant of recovery. Recovery of function in the shuttle-box appears to be determined by general levels of interoperative stimulation.

The finding that general interoperative stimulation increases recovery of function appears to be limited to the shuttle-box situation. Robert

Thompson (1960) found that, in a two-choice discrimination box, successive unilateral damage to the striate cortex without interoperative training resulted in complete loss of a black-white discrimination habit. If, however, a retention test was given between the striate operations, the habit was spared.

This result for a two-choice discrimination was confirmed by Petrinovich and Carew (1969). Petrinovich et al. (1969) and Petrinovich and Bliss (1966), however, found that the size of the lesion was also a major determinant of how the interoperative period affected recovery in the two-choice discrimination. They found that with small lesions, about ten per cent of the cortex, interoperative stimulation affected the retention in the two-choice discrimination in the same way it affected retention in the shuttle-box (i.e. general stimulation spared the habit). With larger lesions, twenty per cent or more, interoperative practice was necessary for recovery.

Kircher, Braun, Meyer, and Meyer (1970) were interested in the capability of amphetamine to aid recovery of function. They injected their rats with amphetamine several times in the period between two large serial ablations. They found no evidence of savings that could have been attributed to the amphetamine injections. It is evident that recovery of function in serial ablation studies is determined by the task, the size of the operation, and the conditions which prevail interoperatively.

A third group of studies have dealt with manipulations to improve recovery of function after bilateral posterior ablations given in adulthood. Braun, Meyer, and Meyer (1966) and Jonason, Lauber, Robbins, Meyer, and Meyer (1970) found that if animals were first trained and then given a posterior cortical ablation, injection of amphetamine aided the recovery of

the task upon retraining. Animals that were not pretrained but received the operation and amphetamine were inferior in their performance when they were compared with the rats that had had pretraining before the operation and the injections of amphetamine. In other words, the amphetamine only aided the performance of rats that were pretrained. This evidence indicates that animals do not lose the memory for a black-white discrimination following a lesion. Rather, it appears that the operation causes the memory to be suppressed and that amphetamine taps the suppressed memory.

The last group of studies was concerned with what specific varieties of experiences could aid in recovery of function after a bilateral posterior cortical ablation. Bauer and Cooper (1964) suggested that the deficit that the striate animal showed was a result of a reduction in its ability to use sensory information from the environment. They postulated that normal animals used both available pattern and luminous-flux cues to learn a black-white discrimination. It was shown that a striate operation resulted in the loss of pattern vision. Therefore, when a striate animal was required to relearn a task that it had acquired pre-operatively, it was using a restricted set of cues; the restriction of cues might have accounted for the lack of savings the striate animals showed. They hypothesized that if a normal animal's acuity was restricted in the original learning of a task the animal would be learning the task under conditions similar to what a striate animal would be exposed. They thought that if a rat's vision was restricted pre-operatively it might result in savings of the task for the animals after a striate lesion. They sutured translucent cups around the eyes of one group of rats to impair visual acuity; they also sutured open rings which did not restrict vision around the eyes of another group of rats. These animals were

trained on a black-white discrimination and then given striate lesions. Following recovery from the operation, the rats were retrained on the black-white task. Their findings were that the translucent cup group showed little decrement but that the open ring group showed marked impairment. This evidence supported the notion that it was a sensory loss that was caused by the striate lesion.

Hamilton and Treichler (1968), drawing upon information in the Bauer and Cooper (1964) study, ran a study in which rats were either given multiple brightness and pattern cues or only brightness cues as discriminanda for a two-choice discrimination task. Since pattern discrimination normally requires a greater amount of visual acuity than brightness discrimination, the Bauer and Cooper interpretation would predict that providing brightness and pattern cues should enhance original acquisition but impair post-operative relearning relative to pre-operative training on brightness cues alone. Hamilton and Treichler found that normal animals with both brightness and pattern cues learned the discrimination faster than the group with only brightness cues; but they found no difference in savings scores as a function of pre-operative training. Contrary to Bauer and Cooper's findings, they found that animals that were given pattern and brightness cues after the operation were superior in their performance when compared to animals that received brightness cues only. This finding was, also, contrary to the studies that found that striate animals could not learn a pattern discrimination. Hamilton and Treichler felt that the superior post-operative performance by subjects on the multiple cue task resulted from differences in the total amounts of luminous flux present in the two different tasks. To test this hypothesis they ran a group of striate rats that received an

irrelevant pattern along with the brightness cue. They found that the irrelevant pattern group's performance was the same as the group in which pattern was a relevant cue. This finding suggested that the superior performance of the relevant pattern group over the brightness only group was a function of the lower flux level inherent in the pattern stimuli and not the result of the animals utilizing the pattern. In other words, low-flux-level tasks were easier for striate animals to learn than high-flux-level tasks. They also thought that an alternative explanation of the results of Bauer and Cooper might be that the rats with the translucent eye cups learned an easier low-flux-level task, while those with open rings learned a more difficult high-flux-level task; and this resulted in the translucent cup group learning faster.

Chow (1951) conducted a study using temporal lesions in monkeys which suggested that training post-operatively could aid recovery of a different task than that which was learned pre-operatively. He reported that monkeys with bilateral temporal neocortical ablations lose learned visual discriminations of color, brightness, and pattern and that they can reacquire these habits after additional training. He was concerned with what could be done after temporal ablations which might facilitate recovery of pre-operatively learned tasks. He trained his animals pre-operatively to make discriminations based on brightness, color, and pattern. He then removed the monkeys' temporal lobes. Following the operation, the monkeys were kept in a dark room, in their home cages, or given training on new discriminations of brightness, color, and pattern. After they went through one of the conditions, they were retrained on the original tasks as a measure of retention. He found a reliable difference between the group that was kept in the dark

and the group that was given post-operative training. The group that was kept in home cages showed improvement over the animals kept in the dark, but the difference was not reliable. Since some lost visual discriminations were recovered without retraining and the degree of recovery appeared to be related to the particular conditions of post-operative visual experience, he concluded that this indicated that the nature of the visual deficit was not a simple loss of memory traces but the result of the specific habit being temporarily suppressed.

In conclusion, the main theme running through the recovery of function literature is that recovery can be facilitated by a number of variables. It also appears, at least in some of the studies, that recovery is brought about, in part, by facilitating access to preexisting memories that were suppressed by the operation.

Statement of the Problem

The results concerning recovery of function following cortical damage seem to indicate that recovery of function can be affected by amphetamines and environmental conditions, including learning and general stimulation. However, there has been little evidence, except for the study by Chow (1951), that environmental conditions can affect recovery after bilateral damage to the adult cortex. The work showing that environmental manipulations are effective in offsetting the deficit caused by infant lesions and serial unilateral lesions suggests that such manipulation would be effective in offsetting the deficits caused by bilateral adult ablations. Evidence from amphetamine studies indicate that recovery can be facilitated after adult bilateral ablations.

The purpose of this study was to find out what kinds of learning situations could, following a striate ablation of the adult cortex, facilitate recovery of a black-white discrimination. A learning situation might be thought of as comprising two aspects that might cause recovery of function. One of the aspects of the learning situation is that an animal is forced to use as discriminative cues specific stimuli in order to solve the problem. The other aspect of the learning situation is that an animal is exposed to irrelevant stimulation. In this experiment, these two aspects of a learning situation were varied to find their effects on recovery of function. All animals were trained to make a black-white discrimination pre-operatively. The animals post-operatively were given specific types of training and then required to relearn the pre-operative task as a measure of retention. Several types of specific stimulation were given. One group of animals post-operatively had to learn a new black-white discrimination. This group was

designed to determine whether requiring an animal to use visual information could cause recovery of visual function. A second group was exposed to irrelevant black-white stimulation. This group was designed to determine whether non-specific visual experience could cause recovery of visual function. A third group of animals was required to make a roughness discrimination in the absence of visual stimuli. This group was designed to determine whether requiring an animal to use non-visual stimuli aided in recovery of visual function. A fourth group of animals received roughness training and was then required to reverse the response it learned pre-operatively. This group was designed to determine whether pre-operative training effected recovery of visual function after bilateral striate damage.

Method

Subjects

The subjects in this study were 50 experimentally naive male Long-Evans rats, weighing 250-400 grams. They were housed in individual cages. In order to reduce extraneous visual stimulation, each cage was enclosed on all sides except for the bottom which was wire mesh. Except for the period of the experiment in which the animals were trained on a food rewarded task, the animals were maintained on an <u>ad lib</u> diet of water and Purina Rat Chow.

Surgery and Histology

All operations were performed under Equi-thesin anesthesia. The intended ablation encompassed all neocortex caudal to the coronal suture and medial to the rhinal fissure. Following incision of the dorsal surface of the scalp, the skull was removed bilaterally from the coronal to the lambdoidal sutures. The dura was reflected and the posterior cortex was removed by aspiration. Post-operatively, all subjects were injected with an antibiotic and returned to their home cages. Seven days were allowed for recovery from surgery.

At the end of testing, the animals were anesthetized with Equi-thesin and perfused with 0.9% saline and 10% formalin. The brains were removed and the dorsal surfaces were photographed. The brains were then embedded in celloidin and sectioned at 30 micra. Every fifth section through the lateral geniculate body was stained with cresyl violet, mounted, and examined for extent of retrograde degeneration in the dorsolateral geniculate nucleus of the thalamus. Diagrams were made of the lesions and the amounts of lateral geniculate degeneration.

Apparatus

One of the training apparatus was similar in construction and dimension to that of Thompson and Bryant (1955). The Thompson-Bryant box was a two-choice shock avoidance discrimination box. It was constructed of black acrylic plastic; and it consisted of a start box, choice compartment, and goal box. The start box was separated from the choice compartment by a guillotine door. The wall separating the choice compartment and the goal box was divided into two parts by a partition which extended 3-1/2 inches into the choice compartment. Each part of the wall, that was separated by the partition, had a 2-1/2 inch square opening into which discriminanda could be inserted. Five inches above the openings was a fluorescent light which was the only light in the room during testing.

The discriminanda were black and white opaque acrylic doors which fit into the wall openings. The discriminanda could be placed in either opening. The floor of both the start box and choice compartment consisted of a stainless-steel grid. A two inch section of the grid in front of the doors could be electrified independently from the rest of the floor. Scrambled shock was used to electrify the floor. The floor of the goal box was made of black acrylic plastic.

The other apparatus was patterned after that of Grice (1948) (Figure 1). The Grice box was also a two choice discrimination apparatus. It consisted of a start box, a six inch entrance alley, a choice compartment, choice alleys, goal boxes, and interchangeable floor sections.
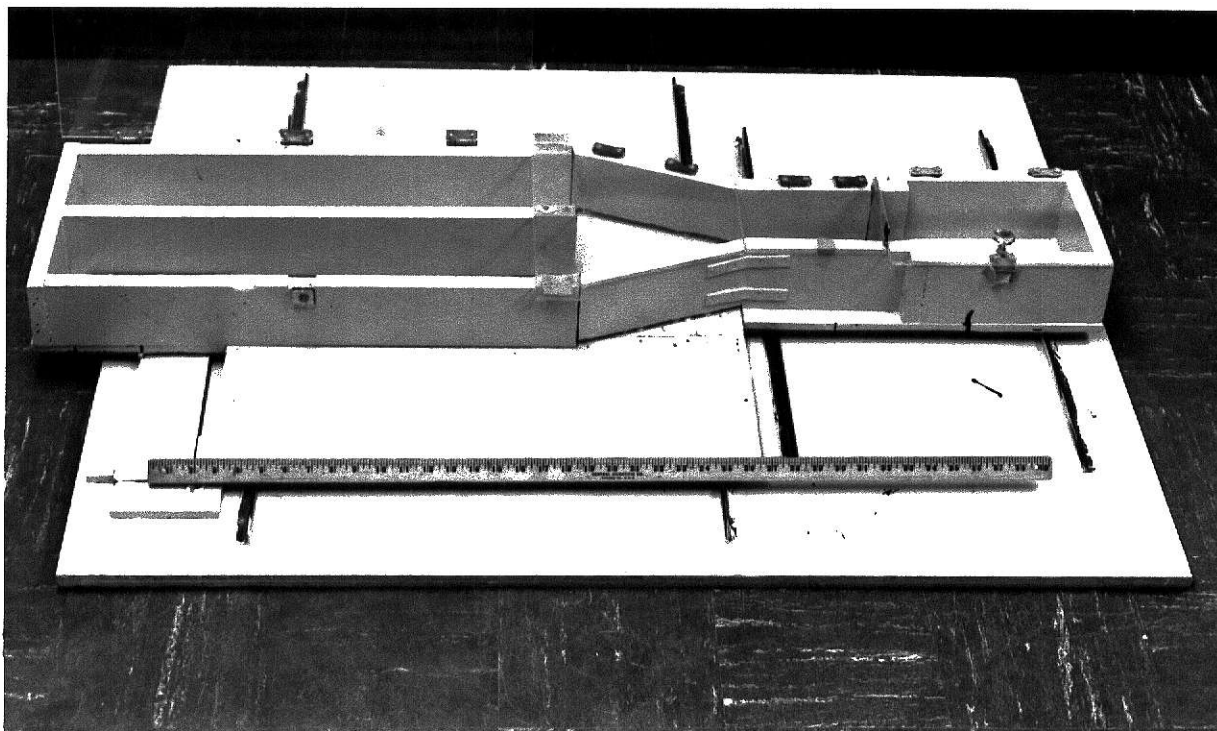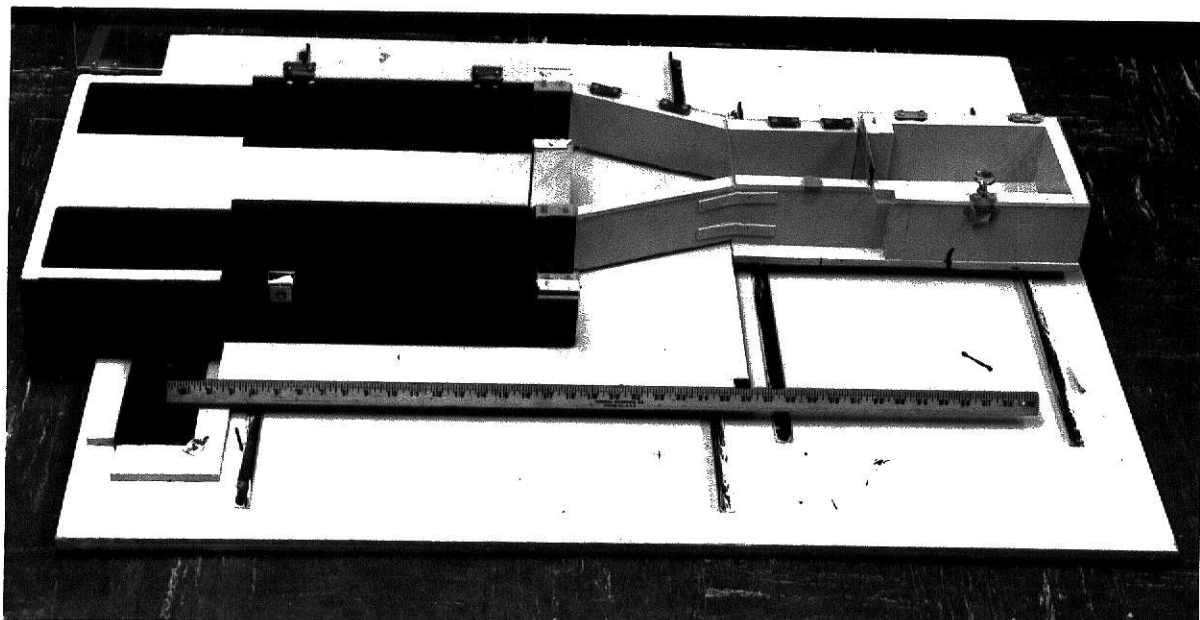
The start box was connected to the choice compartment by a six inch alley which contained a guillotine door. The start box, six inch alley, and the walls of the choice chamber were mounted on a sliding platform which

Figure Caption

Figure 1. Grice box showing the two combinations of interchangeable alleys and floors used in the experiment.

allowed the section to slide left and right. At the end of the choice
chamber, there were two alleys. The alleys were chosen from alleys on one of
two different interchangeable alley sections. One alley section consisted of
three identical alleys. The walls of the outer two alleys were painted black,
and the walls of the middle alley were painted white. The other alley
section consisted of two identical alleys painted gray. There was a goal box
painted the same color as the alley at the end of each alley. There was a
food cup in each goal box.

There were also two interchangeable floor sections which could under-
lie the choice chamber and alley ways. One floor section was smooth wood
painted gray. The other floor section was gray wood, and it was covered with
clear Plexiglas except for a four inch rough strip of sandpaper running
lengthwise down the middle of the floor section. The floors were constructed
so that a rough or smooth floor could underlie an alley at a particular time.
The interchangeable floor section were on slides which allowed the sections
to slide left and right. The floors of the start box and six inch alley were
gray painted wood.

All sections of the Grice box were covered with clear Plexiglas. The
light for the apparatus was supplied by either a 25 watt white light or a
five watt red light covered with additional red filters. Both lights were
about six feet over the choice chamber of the apparatus.

Experimental Design

There were five groups with ten animals in each group (Table 1). Each
group was designated by the sequence of positive stimuli it received. For
example, Group WWW learned to run to the white door in its pre-operative

Table 1

Experimental Design

	Groups				
	WWW	WMW	WRW	BRW	WNW
Positive Cue in Thompson Box Training	White	White	White	Black	White
Surgery	--------------------Striate Lesion--------------------				
Positive Cue in Grice Box Training	White	Matched	Roughness	Roughness	None
Positive Cue in Thompson Box Retraining	White	White	White	White	White

training in the Thompson box, to the white alley in the Grice box, and to the white door in its post-operative training in the Thompson box.

All groups were first trained to discriminate between a black and a white door in the Thompson box. The white door was the positive cue for Groups WWW (white, white, white), WNW (white, no training in the Grice box, white), WMW (white, matched with Group WWW, white), and WRW (white, rough, white). The black door was positive for Group BRW (black, rough, white).

After training in the Thompson box, all animals were given bilateral posterior cortical lesions and allowed to recover. At the end of the recovery period the animals were put on food deprivation and trained on a Grice box task. Group WWW was trained to discriminate between black and white alleys. The white alley was the correct alley. Animals in Group WMW were matched with animals in Group WWW, and they were forced to make the same responses to the stimuli as animals in Group WWW. Groups WRW and BRW were trained to discriminate between two floor textures. Members of Group WNW were maintained in their home cages; they received no Grice box training.

After their training in the Grice box, all groups were retrained to discriminate between black and white doors in the Thompson box. The white door was the correct door for all groups.

Thompson-Bryant Box Training

The procedure that was used was basically the same as the one used by Horel et al. (1966). On the first day of training, subjects were individually placed within the apparatus and left there for fifteen minutes with all doors absent so that the animals could move freely through all compartments. On the second day of training, each subject was placed within the start box. The subject was shocked unless it moved into the choice compartment within

five seconds after the guillotine door opened, and the animal received a
second shock within the choice compartment if it failed to exit through the
goal-box openings within thirty seconds. This procedure was repeated until
the subject made five successive runs into the goal box without getting
shocked at any point. Next, a pair of black doors were inserted which could
be tipped over backwards. The doors filled the lower half of the openings
between the goal box and the choice compartment. The subject was run until
it made another five consecutive avoidances of the shock by exiting within
thirty seconds through the openings. On the third day of training, the
animal was required to make another three consecutive avoidances to the half
doors. Then a full sized black door and a full sized white door replaced the
two black half doors. Four groups of animals learned to exit through the
unlocked white door without first approaching to within two inches of the
locked black door. Subjects that came within two inches of the incorrect
door were shocked. Another group had to learn to exit through the unlocked
black door without first approaching to within two inches of the locked white
door. The trial was over when the subject finally succeeded in escaping from
the choice compartment. The unlocked door appeared to the left and right in
a random sequence. At the end of a trial the subject was returned to a
holding cage, and the next subject was tested. All groups were given twenty
trials a day until they completed nine out of ten consecutive trials without
being shocked.

The post-operative procedure for the task consisted of all groups
learning a black-white discrimination with the white door being positive. On
the first day of retraining, all animals were given three trials with black
half doors followed by thirty trials with full sized black and white doors.

Then the animals were given twenty trials a day until they completed nine out of ten consecutive trials without being shocked in the choice chamber or in front of the negative door. It should be noted that the criterion was less stringent for the retraining on the Thompson-Bryant box task.

Training for the Grice Box

All animals, except for animals in Group WNW, were maintained on a twenty-three hour food deprivation schedule for at least four days before training in the Grice box and continued on the deprivation schedule until training in the Grice box was completed. Animals in Group WNW were maintained on ad lib food and water during this period.

A five watt red light covered with additional red filters was used with Groups WRW and BRW in order to reduce availability of visual cues. All other groups were run under a 25 watt white light. On the first day of training, the rats were placed individually in a gray alley that connected to a gray goal box. The goal box contained 90 mg. of Noyes pellets. A rat was kept in the alley and goal box section for fifteen minutes or until it ate the pellets.

On the second day of training, each animal was placed in a gray goal box and allowed to eat a 45 mg. Noyes pellet which was the standard reward for the rest of the training in the Grice box. Each rat was placed in the goal box three times and allowed to eat a pellet. Then each animal was placed at the start of a gray alley and allowed to run down the alley into the goal box for the food reward three times. Each animal was then placed in the choice chamber and allowed to run to the goal box for the reward three times. An animal was next placed in the start box and allowed to run out of the start box into the choice chamber and down one of the alleys to gain a

reward in the goal box. The rat was forced to alternate randomly running down the left and right gray alleys for reinforcement by means of a clear Plexiglas barrier at the start of one of the alleys. This was done ten times on day two and five times on day three.

After the five forced trials at the start of day three, the groups were trained to their specific stimuli. Group WWW was confronted with a black and a white alley at the end of the choice chamber. The floor was smooth gray wood. The animals had to learn to enter the white alley to obtain food. Group WMW was matched with animals in Group WWW. The animals in Group WMW were confronted with the same stimuli as Group WWW, and they were forced to duplicate the performance of their matched group by means of a clear Plexiglas barrier at the start of one of the alleys. Group WMW received the same number of reinforcements as Group WWW, but the reinforcements were randomly presented with the black and white alleys. Groups BRW and WRW were confronted with gray alleys at the end of the choice chamber; the floor of one of the alleys was rough, and the floor of the other alley was smooth. The rough and the smooth floors were presented randomly left and right. Due to the low levels of red illumination, it was assumed that any discrimination learned was a tactile discrimination. The rats in these two groups had to learn to run down the alley with the rough floor for the food reward. Animals in Group WNW were maintained in their home cages and received no Grice box training.

After pretraining, the training to the positive cues was started. Each animal was placed in the start box and the guillotine door opened. This allowed the animal to run into the choice chamber and down an alley into a goal box. If the animal ran down the alley having the positive cue, without

first entering the goal box of the alley having the negative cue, it was reinforced and placed back in a holding cage; and the next animal was tested. If the animal ran down the negative alley and into its goal box, it was not reinforced; and it was run again until it made the correct response. The animal was then placed back into a holding cage, and the next animal was tested. Each rat was given twenty trials a day until it completed nine correct out of any ten consecutive trials.

Each time a rat was placed in the start box and allowed to run to a goal box was defined as a sub-trial. A trial consisted of as many sub-trials as were necessary for the rat to run down the alley with the positive cue. A correct trial consisted of the animal running down the alley with the positive cue on the first sub-trial of a trial without first entering the goal box in the negative alley. This type of procedure was used to reduce position preference from developing.

The day the animal reached the criterion, it was given ten additional trials and placed on ad lib food and water. The next day the rat started relearning the Thompson-Bryant box task.

Results

Diagrams of the lesions and the amount of lateral geniculate degenera-
tion are presented in Figure 2. There appears to be no consistent difference
between the groups in the size of the lesion or in the amount of lateral
geniculate degeneration. The sparing of the lateral geniculate that was
found occurred on the dorsolateral margins of the lateral geniculate bodies.
There was also extensive degeneration found in the nucleus lateralis thalami
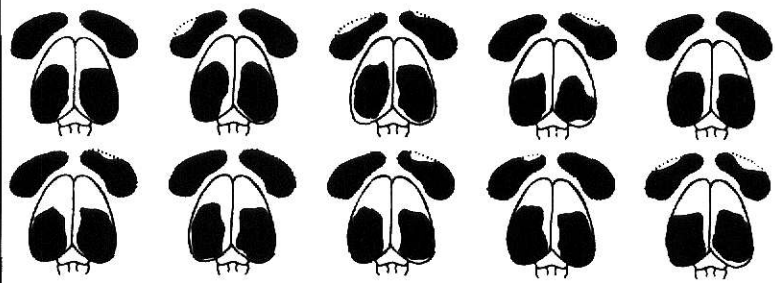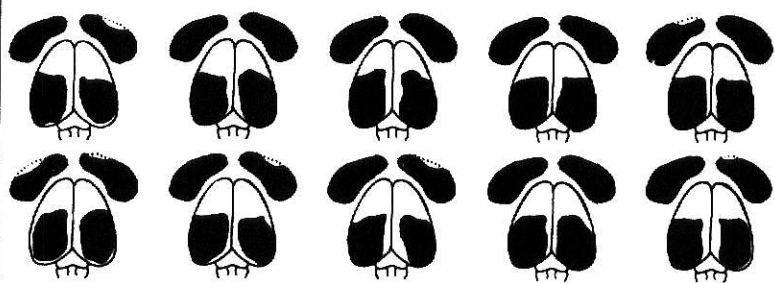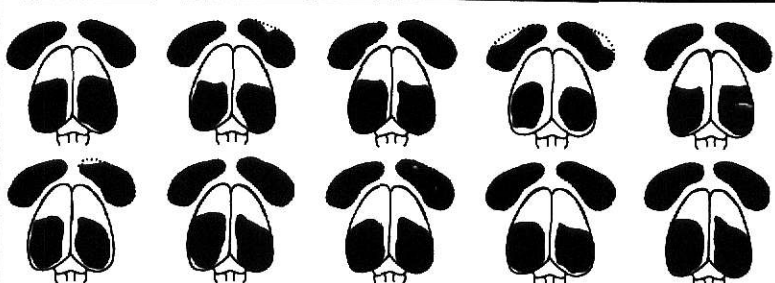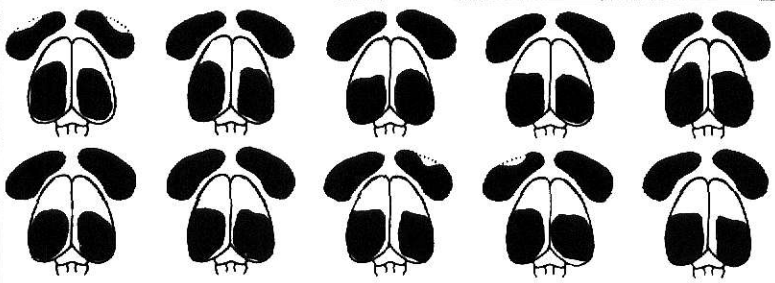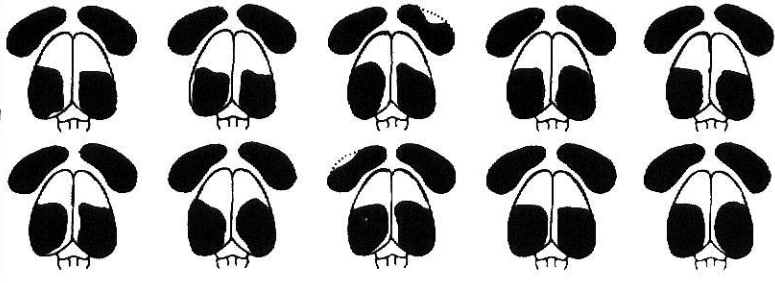pars lateralis and in the nucleus ventralis thalami in all animals.

The mean numbers of trials required for learning in the Thompson box
pre and post operatively and for the learning in the Grice box post-
operatively are presented in Table 2. The mean difference scores between the
pre and post operative learning scores for the Thompson box are also
presented in Table 2. A comparison of the difference scores revealed that it
took animals in Groups WWW, WMW, and WRW less trials to relearn the task
after the operation, and the difference scores also revealed that it took
animals in Groups BRW and WNW more trials to relearn the task after the
operation.

A one-way analysis of variance performed on the original learning
scores for the Thompson box revealed that there were differences between the
five groups (F = 3.704, df = 4/45, p < .01). Newman-Keuls tests revealed
that Group WNW differed reliably from Groups WMW and WWW (p < .01). Yet,
there were no reliable differences between Groups WWW, WRW, BRW, and WMW nor
between Groups BRW, WRW, and WNW.

This experiment took several months to run and all of the groups were
not started at the same time. Groups WWW and WMW were started first followed
by Group WRW and then by Group BRW. Group WNW was added at the end of the

Figure Caption

Figure 2. Diagrams of the cortical lesions and lateral geniculate nucleus degeneration.

WWW

WMW

WRW

BRW

WNW

Table 2

The mean number of trials for each group to reach a 9/10 criterion for the pre-operative Thompson box, post-operative Grice box, and post-operative Thompson box tasks, and the mean difference scores between the pre-operative and post-operative training in the Thompson box. A positive difference score indicates a greater mean trial to criterion.

Groups	Pre-operative Thompson Box Means	Post-operative Grice Box Means	Post-operative Thompson Box Means	Difference Scores Means
WWW (white, white, white)	49.7	35.1	22.1	-27.9
WMW (white, matched, white)	50.0	--	32.2	-21.6
WRW (white, rough, white)	44.4	38.2	25.4	-19.0
BRW (black, rough, white)	39.7	35.3	51.2	+11.5
WNW (white, no Grice box, white) training	37.3	--	49.4	+13.3

$p < .01$

experiment. The Newman-Keuls tests revealed this order effect in that groups started in the middle of the experiment (Groups WRW and BRW) did not differ from groups started in the first part or last part of the experiment, and groups started in the first part of the experiment (Groups WWW and WMW) did differ from the group started at the last of the experiment (Group WNW). The most reasonable explanation for these differences is that the experimenter increased his ability to train animals in the particular apparatus as the experiment progressed.

Since there were differences in the performance of the animals pre-operatively, difference scores between the pre-operative and the post-operative learning scores were used to assay the effect of the Grice box training on the relearning of the Thompson box. Since learning and relearning in the Thompson box were fairly close in time for any particular animal, the effects due to experimenter learning would be at a minimum. Therefore, the difference scores would reflect most accurately the effect of the Grice box training on the relearning scores for the Thompson box. The difference scores revealed that there were no differences in the learning in the Thompson box post-operatively between groups that had Grice box training post-operatively in conjunction with training to go to white in the Thompson box pre-operatively. The groups that differed in their performance from the above three groups either had training to go to black pre-operatively or did not receive any training in the Grice box post-operatively. The difference scores revealed that there were reliable differences between the five groups ($F = 10.463$, $df = 4/45$, $p < .00001$). The Newman-Keuls tests revealed that there were no reliable differences between Groups WWW, WMW, and WRW. The tests also showed that there were no reliable differences between Groups WNW

and BRW. However, the test did show that there was a reliable difference between Groups WWW, WMW, and WRW and the Groups WNW and BRW (p < .01).

A one-way analysis of variance revealed there were no reliable differences between groups in the animal's ability to reach the nine out of ten criterion for the Grice box tasks.

Group learning curves were plotted after the method described by Horel et al. (1966). Individual learning functions were obtained by determining the number of trials it took each subject within a group to reach the block of 10 trials in which it made one through nine correct responses to the discriminanda. The last 10 trials were not included in the scores averaged to obtain the functions. Computation of each point on the curve was obtained by finding the number of trials required by each subject to meet each of the nine successive criteria and then averaging the scores within the groups for each criterion. The pre and post operative learning functions for each group are presented in Figure 3. The pre and post operative learning functions for all groups are presented in Figure 4.

The learning functions for Group WNW are presented in Figure 3A. These data indicated that it took the animals a few more trials to relearn the task post-operatively than it did to learn the task pre-operatively. These data of Group WNW also indicated that striate lesioned animals started at a higher initial criterion than normal animals, but showed a relatively lower rate of learning than that of normal animals as training progressed. The BRW group's learning functions (Figure 3B) approximated the learning functions of Group WNW.

The learning functions for Groups WWW, WRW, and WMW (Figures 3C, 3D, and 3E) were similar to each other but quite different from the learning

Figure Caption

Figure 3. Pre and post operative learning functions for each group in the Thompson-Bryant box with lines indicating one standard deviation from the criterion means.

GROUP
WNW

GROUP
BRW

GROUP
WWW

GROUP
WRW

GROUP
WMW

PRE-OP LEARNING FUNCTION
POST-OP LEARNING FUNCTION
S.D. PRE-OP
S.D. POST-OP
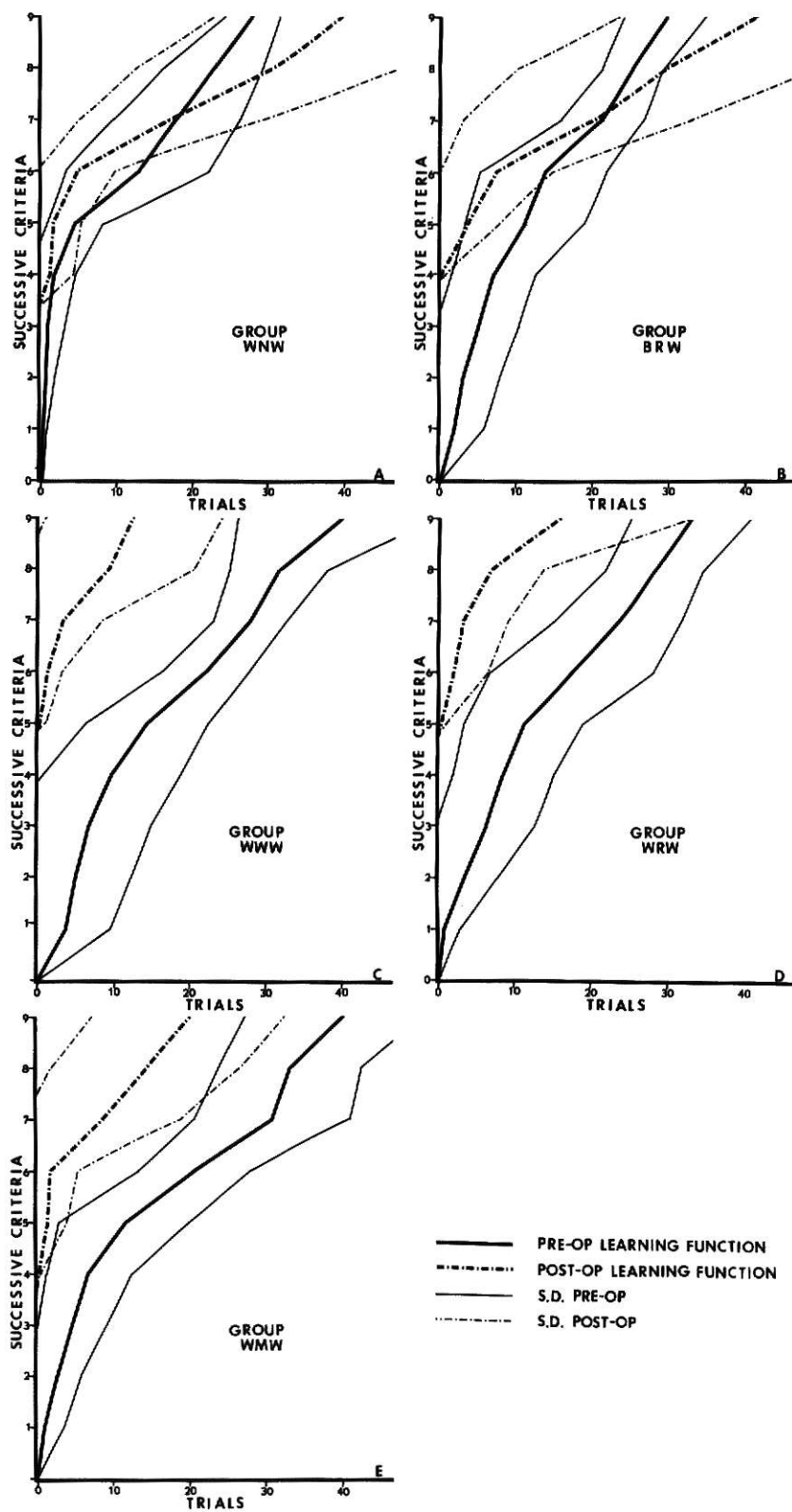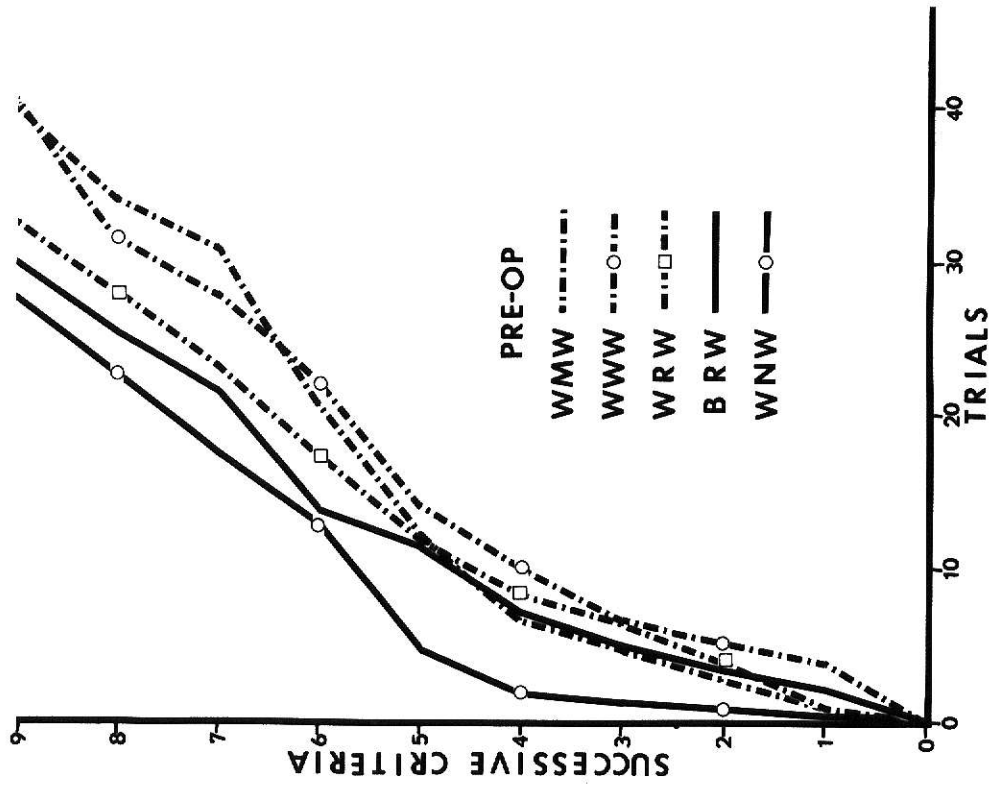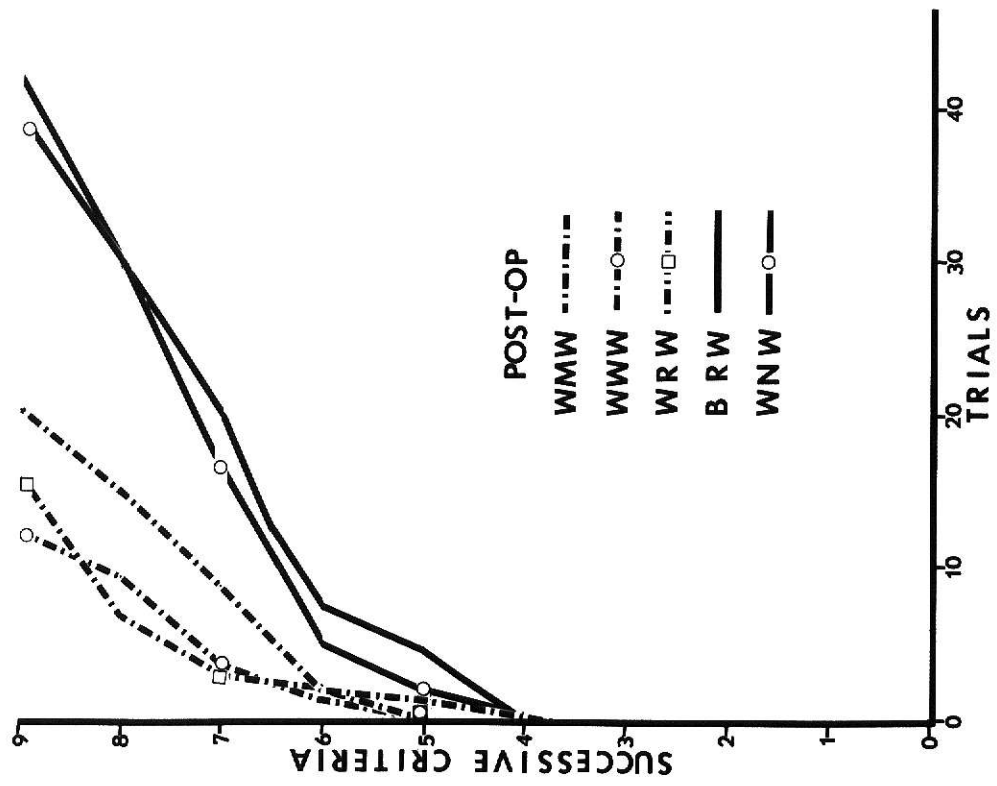
Figure Caption

Figure 4. Combination of the pre and the post operative learning functions in the Thompson-Bryant box for all groups.

POST-OP

WMW ·-·■·-·
WWW ·-·○·-·
WRW ·-·□·-·
B RW ———
WNW ——○——

TRIALS

SUCCESSIVE CRITERIA

PRE-OP

WMW ·-·■·-·
WWW ·-·○·-·
WRW ·-·□·-·
B RW ———
WNW ——○——

TRIALS

SUCCESSIVE CRITERIA

functions of Groups WNW and BRW. The learning functions for these three groups showed that animals initially met a higher criterion than normal animals, and that they reached the higher criteria more quickly.

The different types of training in the Grice box post-operatively produced almost identical results for the relearning of the Thompson box post-operatively for the three groups of animals that were trained to go to white pre-operatively (Groups WWW, WRW, and WMW). Animals that had different pre-operative training than these three groups (i.e. learning to go to black pre-operatively and roughness training post-operatively, Group BRW) or had no Grice box training (Group WNW) were different from the above three groups both in the number of trials it took them to relearn the Thompson box and in the general shape of the relearning functions.

Discussion

The performance of animals in the group that received no post-operative experience in the Grice box but did receive training in the Thompson box pre and post operatively was comparable to the findings of Horel et al. (1966) in that the striate lesioned animals started at a higher initial criterion than normals, but showed a relatively lower rate of learning than that of normal animals as training progressed.

The performance of the other groups in this experiment suggests several conclusions about the effects of experience on recovery of function. Groups that received the same pre-operative training and some kind of post-operative experience in the Grice box were comparable in their relearning of the Thompson box (Groups WRW, WMW, and WWW). All three of these groups relearned faster in the Thompson box than the group that received no Grice box training (Group WNW). This suggests that simple exposure to visual stimuli (Group WMW), learning a task in a non-visual modality (Group WRW) and learning a task in a visual modality (Group WWW) similarly aided in the recovery of function. That these three groups are comparable in their performance in the Thompson box, even though they had received different varieties of stimulation in the Grice box, suggests that general types of post-operative stimulation are effective in aiding in recovery of function.

The effects of the first post-operative training can be explained in two ways. The first explanation would maintain that training in the Grice box allowed an animal to adjust to the cortical damage in such a way as to allow it to learn the second post-operative task quickly. The second explanation would maintain that the Grice box training allowed the animal access to some pre-operative information which the animal used to solve the second

post-operative task. In other words, the training allowed the animal to use specific pre-operative information after the operation to solve the problem.

Several lines of evidence support the second interpretation of the results. One line of evidence comes from the comparison of groups that received the same post-operative treatment but different pre-operative experience (Groups BRW and WRW). Since these two groups received the same post-operative training, any differences in the performance of the two groups post-operatively would reflect the effects of the pre-operative training. In other words, if the two groups differed in their post-operative performance, it would mean that some aspect of the pre-operative training survived the operation. Further, if there was survival of the habit through the operation, it would be expected that upon relearning the Thompson box task, the group that had to reverse its responding to the stimuli (Group BRW) would do worse than the group that did not have to reverse its responding to the stimuli (Group WRW). As was noted earlier, these two groups differed in relearning in the Thompson box both in trials to criterion and in the general shape of their learning functions. Also, the group that had to reverse its responding to the stimuli relearned the task more slowly than the group which did not have to reverse its responding to the stimuli. This would indicate that pre-operative training had a definite effect upon relearning the task post-operatively.

Another line of evidence that suggests that post-operative training allowed access to pre-operative information was the performance of Group WMW. This group was trained with random pairing of food with position and brightness. Rescorla (1967) suggests that animals presented with random irrelevant stimuli in a task learn that the random stimuli are not relevant for the

solution of the task. Thus, if formerly random stimuli become relevant for the solution of the task, the animal is impaired in learning the task because it first has to overcome the training that the stimuli are irrelevant before it can solve the task. If Rescorla's notion is correct and it is assumed that the Grice box training does not reestablish pre-operative information, then it would be expected that the performance of Group WMW on the second post-operative task would have been worse than Groups WRW and WWW. Animals in Group WMW would have to overcome the training that visual cues were irrelevant before they could solve the task and animals in the other two groups would not. If, however, it was assumed that the Grice box training reestablished the pre-operative habit, it would be expected that the animals in the three groups would be comparable in their performance on the second post-operative task. As was noted earlier, the performance of animals in the three groups was comparable. Therefore, the second explanation is more appropriate.

If recovery of memory was complete for operated animals that received stimulation after the operation, it would be expected that animals in the group that had recovery of the habit and then had to reverse their responding to the stimuli (Group BRW) would do worse than animals in the group that had to relearn the task without recovery of the habit (Group WNW). As was noted earlier, animals in Group BRW were comparable in their performance to animals in Group WNW. In other words, the expected difference was not found. This information could have two implications. It could mean that animals in Group BRW which received the roughness discrimination training in the Grice box did not have a recovery of pre-operative memory, and therefore the reason the two groups were comparable was that they started out at the same place in

their relearning in the Thompson box. The other implication would be that while recovery did occur in Group BRW there were several facets of the post-operative Thompson box situation that masked the expected effects of recovery, making the performance of animals in Group BRW comparable to the performance of animals in Group WNW. Several lines of evidence suggest that the second interpretation would be reasonable to assume. It has been established that normal animals use both available pattern and brightness cues as stimuli to solve a brightness discrimination (Hamilton and Treichler, 1968; Bauer and Cooper, 1964). It has also been established that posterior decorticated animals can not use pattern cues (Tsang, 1937b; Thompson, 1970). Since striate lesioned animals lose the ability to use pattern cues, it could also be assumed that the stimulation after an operation only causes recovery of the ability to use brightness memory and not the ability to use pattern memory. Thus, if operated animals that have recovered pre-operative memory were required to reverse a response acquired pre-operatively, they would only have to reverse their responding to brightness cues while normal animals that have to reverse a response would have to reverse their responding to pattern cues as well as brightness cues. This would mean that operated animals would be able to reverse a response faster than normal animals. This would tend to minimize the effect of the recovered memory in the performance of Group BRW. However, if operated animals that have recovered pre-operative memory were not required to reverse a pre-operative response but were required to relearn the same response post-operatively, the ability of the animals to use pre-operative brightness information would facilitate the relearning of the response post-operatively.

Another observation that might account for the lack of difference between Groups BRW and WNW is that striate lesioned animals have a preference

for white after the operation (Thompson, 1970). The tendency for animals in Group BRW to run to black based on recovered pre-operative memory would come in conflict with the operated animal's tendency to go to white. This would tend to minimize the effect of the recovered pre-operative memory in the performance of Group BRW. Therefore, the ability of the striate lesioned animals to reverse a response faster than normals and the tendency of the striate lesioned animals to run to white masks the effect of the recovered pre-operative memory on the performance of Group BRW and causes the perform- ance of Group BRW to be comparable to the performance of Group WNW. Since the difference between Groups BRW and WNW would be small, the task used in this experiment might not have been sensitive enough to show the difference.

The evidence in this experiment appears to be consistent with the hypothesis that training on a task and general stimulation post-operatively reestablishes some pre-operative information. There are several other experiments that are consistent with this type of hypothesis. Braun et al. (1965) found that injections of amphetamine following bilateral posterior decortications in rats improved only the performance of animals that had pre-operative experience with the task. Stratton (1972) trained rats pre- operatively to make simultaneous and successive brightness discriminations. She then removed the posterior cortex and retrained the rats to make the same two discriminations. She found that retention scores for the first post- operative task yielded zero savings. She found, however, that on the second post-operative task the animals showed savings reliably different from zero. In the two above experiments, stimulation after bilateral cortical damage could be interpreted as causing recovery of pre-operative information.

If general stimulation after bilateral cortical damage does cause recovery of pre-operative information, there are two major conclusions that

can be drawn. First, since it has been established that the cortex is not the site for relearning of brightness habits after bilateral posterior decortications (Horel et al., 1966), the evidence in this experiment suggests that subcortical structures must be involved in the learning and storage of habits. Second, these data also suggest that two variables must determine the rate of learning and the shape of the learning function of animals that are trained after bilateral cortical damage. One variable is the learning and/or the relearning of the task by the animal. Since this experiment demonstrates that training and general stimulation cause recovery of pre-operative information, the general stimulation involved in training an animal after an operation must reestablish some pre-operative information which would affect the learning of the task. Therefore, the learning variable and the recovery variable must interact to determine the rate of acquisition of a habit after striate damage.

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EFFECTS OF TRAINING ON RECOVERY OF
FUNCTION IN STRIATE RATS

by

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Following posterior decortication, the effects of training on the recovery of a pre-operatively learned black-white habit were analyzed. Random black-white stimulation, roughness discrimination training, and training on a new black-white discrimination had the similar effect of enhancing relearning of the pre-operative task. Animals given no stimulation before they had to relearn the pre-operative task or animals that received roughness discrimination training and then had to make a discrimination reversal post-operatively showed no enhancement in relearning the pre-operative task. It was concluded that general training after posterior decortication causes recovery of pre-operative memory in rats.