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THE EFFECTS OF TEMPORAL NEOCORTICAL INJURIES ON THE
LEARNING AND RETENTION OF PATTERN DISCRIMINATIONS IN THE RAT

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

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* * * *

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1984

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INTRODUCTION

Approximately forty years ago, Harlow and his colleagues carried out a series of studies which were aimed at determining why complex common objects are more readily discriminable by monkeys than other visual cues (Harlow, 1944, 1945a, 1945b, 1945c, 1945d; McClearn and Harlow, 1954; Schrier and Harlow, 1954; Schuck, 1960; Warren, 1953; see Meyer, Treichler, and Meyer, 1965 for review). Their general strategy was to train the animals on many different kinds of visual tasks. They observed that whether a discrimination problem is easy or hard for a monkey had little to do with the color, form or size of the cues. Instead, they observed that the variable which had the greatest effect upon performance was whether the animal would touch the cues to be discriminated.

That result is now described as the stimulus-response spatial contiguity effect. Its power was elegantly demonstrated by a study of Schrier and Harlow (1957). Normal monkeys were trained in a WGTA on a red-green discrimination. The relevant stimuli were small red and green squares placed or attached to larger white plaques. In the "part-card" condition, the white plaques were fixated to the form board and the smaller red and green stimuli were merely placed upon the center of the plaques over the foodwells. Thus, the monkeys were required to displace the small red and green squares to reveal the
reward. In the "whole-card" condition, the white plaques could be moved freely but the relevant red and green stimuli were fixated to the plaques. Monkeys in this condition were required to move the whole plaque to reveal the reward.

The "part-card" condition was by far the easier of the two. For example, in the "whole-card" condition, the animals never achieved performances of better than 60 percent correct. Those monkeys performed very poorly because their responses were spatially discontiguous from the relevant stimuli. Monkeys typically touch the nearest portion of the stimulus plaques when displacing them. Thus, in the "whole-card" condition, the subjects when displacing the stimuli would touch the irrelevant white portion of the stimulus plaques. In the "part-card" condition, the animals are forced to touch the relevant red and green portion of the stimulus plaques.

Schrier and Harlow (1957) also studied the effects of reversals of the two contiguity conditions. The performances of "whole-card" subjects improved very rapidly when they were switched to the "part-card" condition. Subjects in the "part-card" condition when switched to the spatially-discontiguous "whole-card" condition maintained their high performance. Stollnitz (1965) explained the latter observations by arguing that monkeys given training in the spatially-contiguous condition develop observing responses which are maintained when the relevant stimuli are made spatially discontiguous (see also, Wycoff, 1952).
Schuck (1960) replicated and extended the results of Schrier and Harlow (1957). Following training under the "part-card" and "whole card" conditions, he trained monkeys using stimuli where the relevant cues were placed either on the near edge (contiguous condition) or the far edge (discontiguous condition) of the stimulus plaques. The stimulus plaques were locked on one side so that the monkeys were required to push the plaques to uncover the foodwell. Many color discriminations were presented, each for 6 trials. Schuck found that the animals performed at chance when the relevant cues were placed on the far edges of the plaques, but did very well when the relevant cues were on the near edges of the plaques.

An examination of the stimulus plaques employed in these studies illustrates the powerfull effects of small changes in S-R spatial contiguity. The effects were observed when the relevant cues on the far edges of the stimulus plaques were only two and one-quarter inches from the near edges of the stimulus plaques and when the relevant cues on the "part-card"-"whole card" stimuli were only three-quarters of an inch from the near edges of the stimulus plaques.

Experiments on monkeys have also shown that the S-R spatial contiguity effect is enormously enhanced by injuries to the inferotemporal (IT) neocortex (Butter and Hirtzel, 1970; Meyer, 1958, 1972). Temporal monkeys can solve a two-color discrimination as quickly as normals (Butter and Hirtzel, 1970; Mishkin, 1954; Mishkin and Pribram, 1954; Ungerleider and Pribram, 1977), but it is virtually impossible to train a bitemporal monkey on a two-color problem if the
color cues are surrounded by identical white borders (Meyer, 1958). However, temporal monkeys that are preoperatively trained on spatially contiguous and discontiguous versions of a color problem perform at levels that are far superior to those of preoperatively-naive monkeys (Meyer, 1972). That result suggests that monkeys given extensive training on a color discrimination task while they are normal develop observing responses that survive temporal injuries.

Butter and Hirtzel (1970) trained IT monkeys on a color discrimination problem where the relevant stimuli were placed on the far half of the stimulus plaques. They observed that the animals exhibited severe impairments compared to controls but eventually learned the discrimination to the established criterion. The monkeys were then trained with stimuli in which the relevant stimuli occupied less and less of the area of the stimulus plaques. Their performance was unimpaired despite the increasing difficulty of the task. Thus, as in the Schrier and Harlow (1957) experiment, after the monkeys had successfully learned to search for the relevant cues, increasing the spatial separation between the cues and the animals' response sites had no effect.

Monkeys with IT injuries also exhibit impairments of learning and remembering certain kinds of visual-pattern problems (Mishkin, 1954; Mishkin and Pribram, 1954). Typically the monkeys perform as well as normals in discriminating colored stimulus plaques, but fail when they are tested for discriminations of a plus and a square that are mounted on the centers of stimulus plaques. The latter impairments have been
attributed to deficits in complex visual memory (Gross, 1973; Mishkin, 1972). However, such results are due to impairments of attending. The IT preparations have an exaggerated tendency to focus their attention to the area surrounding their hands when making a response. Thus, for visual-pattern discriminations, the subjects are likely to focus upon the irrelevant portion of the stimulus plaque when they make their choice by pushing the plaque's nearest edge.

The fact that bitemporal monkeys can learn to discriminate common-use object problems as readily as normal subjects, provided the animals touch the two objects (Mishkin, 1972), suggests that these animals do not have impairments in complex visual processing. However, such discriminations become very difficult if the objects are attached to plaques and the animals respond to the plaques (Ungerleider and Pribram, 1977).

Lashley (1938) demonstrated that the S-R contiguity effect applies to rats as well. He trained rats to discriminate a square versus a diamond in a jumping stand. After reaching criterion, the lower halves of the stimuli were blackened. The subjects' performance then immediately fell to chance levels. Lashley concluded that "...the lower or inner margins of the figures most frequently determine the reaction...." (Lashley, 1938, p. 152). Ehrenfreund (1948) also found that in rats, performances of simple discriminations may fail when the relevant cues are displaced as little as two inches from the animals' response sites. These data suggest that normal rats tend to focus their attention to the area surrounding their noses when making
Thus, like normal monkeys, normal rats are powerfully effected by spatial discontiguities.

Horel and Stelzner (1979) have identified a cortical area in the rat that they believe is homologous with the inferotemporal cortex of primates. We recently undertook an investigation to determine if bilateral ablations of this cortical area in the rat would enhance the effects of S-R discontiguity (Cloud, Meyer, and Meyer, in preparation). Rats were either subjected to bilateral temporal injuries, bilateral visual injuries, or else served as normal controls. Subgroups of each condition were either trained on S-R contiguous or discontiguous tasks. The animals were trained in a Thompson-Bryant (1955) apparatus and were required to push open doors that were hinged at the top to enter the goal box. In the contiguous condition, the doors (3 1/2" x 3 1/2") were gray except for a 3/4" black or white stripe along their bottom edge. Therefore, the animals would typically touch the relevant stimuli as they entered the goal box. In the discontiguous condition, the same stimuli were inverted so that the black and white stripes were along the top edge.

The results showed no significant differences between the performance of normal, visual, and temporal groups in the S-R contiguous condition. Also, there were no significant differences between the performances of normal and visual lesioned animals in the S-R discontiguous condition. However, both groups found the latter problem to be very difficult to learn, thus they required approximately twice as many trials to meet the criterion as subjects
in the S-R contiguous condition. But the temporal subjects found the
discontiguous problem to be so difficult that the majority failed to
reach the established criterion of performance.

Temporal rats, like monkeys, can solve a simple visual task as
quickly as normals, but if the same stimuli are placed spatially
discontiguous from the response, the temporal subjects exhibit
enormous impairments. Moreover, this effect is not dependent upon the
primary visual areas. Thus, subjects with injuries to the visual
neocortex can solve a S-R discontiguous task as well as normals.

In the second phase of the experiment, the animals were trained
on the same problem but the condition of contiguity was reversed. All
groups demonstrated excellent transfer to the reversed condition.
Even subjects with temporal injuries required only a few trials to
reach criterion when switched to the discontiguous condition. These
results parallel the findings of Schrier and Harlow (1957) with normal
monkeys and of Butter and Hirtzel (1970) with IT monkeys that
increasing the spatial discontiguity has little effect upon
performance once an animal has successfully established the correct
observing response. Also, temporal rats that had never reached
criterion of learning under the S-R discontiguous condition showed
excellent transfer when switched to the S-R contiguous condition.
These subjects were apparently learning the discrimination in the
original condition but could not express that learning in their
performance until the stimuli were made spatially contiguous with
their responses.
In the third phase of the experiment, the animals were subjected to a stringent test of form perception. If temporal animals have deficits in complex visual processing, that impairment should be reflected in their performance on the oblique-stripes problem. Animals can only solve this discrimination by detecting the different orientations of the lines. The stimuli occupied the entire opening, and thus, were spatially contiguous with the animals' responses. Rats with injuries to the visual neocortex have repeatedly been shown to fail to acquire this discrimination (Horel, Bettinger, Royce, and Meyer, 1966; Lavond and Dewberry, 1978). The results of this study revealed no significant differences in the performance between normal subjects and subjects with temporal injuries. In contrast, all of the animals with visual injuries failed to reach the established criterion of performance.

The study has demonstrated a double dissociation between the functions of the visual and temporal neocortex in the rat. Subjects with visual injuries failed the test of form perception but performed like normals in discriminating a spatially discontiguous problem. Subjects with temporal injuries were greatly impaired in discriminating a spatially discontiguous problem, but performed like normals on the test of form perception.

The present investigation further explored the temporal neocortex in the rat by pursuing several questions stimulated by those results. The first question was what would be the effects of temporal injuries in the rat on the discrimination of visual patterns traditionally used.
in primate studies when the cues are presented under either S-R contiguous or discontiguous conditions? The prediction was that the temporal rats would solve the pattern problem as fast as normals under the S-R contiguous condition but would be severely impaired if the same patterns were presented under the spatially discontiguous condition. The fact that the problem involved patterns was expected not to make any difference on the grounds that the deficits, according to our theory, have nothing to do with pattern vision.

We also asked if the conditions of contiguity were then reversed, would the temporal animals exhibit the excellent transfer, as they did for the brightness discrimination problem? The temporal rats were predicted to perform like normals, including the case where temporal subjects were switched from a contiguous to a discontiguous version of the pattern problem. The observing responses established during original learning should permit rapid relearning for both normal and temporal subjects.

The final question was what would be the effects of temporal injuries upon the retention of a preoperatively learned pattern discrimination problem? In primate studies, temporal animals preoperatively-trained on both spatially contiguous and discontiguous versions of a discrimination problem perform much better on the spatially discontiguous problem than preoperatively-naive subjects (Meyer, 1972). Thus, in monkeys, the observing responses appear to survive the temporal injury. However, other primate studies have shown retention deficits for spatially discontiguous pattern
discriminations following temporal injuries, but those deficits are rarely as large as the impairments exhibited by those subjects for original training on a discontiguous visual-pattern problem (Iwai and Mishkin, 1969; Mishkin and Pribram, 1954; Zola-Morgan, Squire, and Mishkin, 1982). Also, in the latter investigations, the animals were not preoperatively trained on the pattern task where the cues are presented contiguously. In the present investigation, temporal rats preoperatively trained on the pattern discrimination in both conditions of contiguity are predicted to be unaffected postoperatively by spatial discontiguity.
METHOD

Subjects

Male Long-Evans hooded rats, 90-120 days of age at the beginning of training, were employed. The 72 subjects were housed in individual cages and were maintained on an ad-lib food and water schedule.

Apparatus

Training was conducted in a version of the Thompson-Bryant (1955) apparatus which consisted of a startbox, a choice compartment, and a goal box. A vertical partition with two 3 1/2" x 3 1/2" (8.9 cm x 8.9 cm) square openings separated the choice compartment from the goal box. The walls of the apparatus as well as the vertical partition were constructed of black plexiglass. The startbox and choice compartment were illuminated by a group of small fluorescent lamps that were attached to transparent plexiglass lids. The floors of the start and choice compartments were made of stainless steel bars from which weak motivating shocks could be administered. The openings to the goal box were fitted with stimulus doors hinged at their top with Velcro. The plus and square patterns were made of 1/2" (1.3 cm) strips of white contact paper centered upon the lower half of black doors. The stimuli could be inverted so that the patterned stimuli were positioned at the top half (discontiguous condition) or the
bottom half (contiguous condition) of the opening to the goal box.

Pretraining and Training Procedures

The animals were first handled for at least 5 minutes per day for 4 days. On Day 5, each animal was permitted to explore the apparatus for 15 minutes. Next, on Day 6, pretraining began, and each subject was trained to run into the goalbox to avoid mild foot shocks. Gray pretraining doors were gradually fitted into the square openings of the partition so that the rats pushed up one of the pretraining doors to enter the goalbox. On Day 7, original training began, and the doorways were fitted with the doors with the plus and square patterns. The spaced-trial training method of Glendenning (1972) was used, which limited the number of trials to 25 per day with a 10-minute rest following the 8th and 16th trials. The correct stimulus throughout all phases of the experiment was the door with the plus pattern whose right–left position was governed by a Gellerman (1933) series. A latch at the rear locked the incorrect door, requiring the subject to enter the goalbox only by pushing up the correct door. Training was continued until the subject had reached a criterion of 9 correct responses in 10 trials. If a subject had not reached the established criterion within 200 trials, training was terminated.

Experimental Design

The subjects were randomly divided into 6 groups, each group consisting of 12 subjects: Group NNC - Normal animals orginally
trained in the contiguous condition; Group NND - Normal animals
originally trained in the discontiguous condition; Group NTC - Normal
animals originally trained in the contiguous condition that
subsequently sustained bilateral temporal injuries; Group NTD - Normal
animals originally trained in the discontiguous condition that
subsequently sustained bilateral temporal injuries; Group TTC -
Animals originally trained in the contiguous following bilateral
temporal injuries; Group TTD - Animals originally trained in the
discontiguous condition following bilateral temporal injuries.

In Phase I the subjects were trained on the plus-square problem
in either the spatially contiguous or discontiguous condition. In
Phase II, the animals were trained on the same problem but the
condition of contiguity was reversed. Following Phase II, Groups NTC
and NTD sustained bitemporal injuries. In Phase III, subsequent to a
12 day recovery for Groups NTC and NTD and a 12 day rest for the
remaining animals, a test of retention was administered to all the
groups on the plus-square problem in the original condition of
contiguity. At the conclusion of Phase III, the animals were trained
in a study whose results will not be reported at this time. When the
training was completed, the animals were sacrificed for histological
analysis.

Surgical Procedures

The surgeries were performed with clean technique while the rats
were under deep anesthesia induced by sodium pentobarbital. The
Injuries were intended to bilaterally encompass the area of the temporal neocortex in the rat as defined by Horel and Stelzner (1979). The ablations were accomplished by aspiration. Following the surgeries, the subjects were given a broadband antibiotic and allowed a 12 day rest period for recovery.

**Histological Procedures**

The subjects at the completion of training were given lethal doses of sodium pentobarbital and were then perfused through the heart with normal saline followed by 10 percent Formalin. The extents of the cortical lesions of the surface were drawn on standard Lashley diagrams. The brains were froze and sectioned at 50u. Every 10th section through the cortical lesion will be mounted and stained with cresly violet. There after the posterior thalamic nuclei were studied to determine the extent of retrograde degeneration.
RESULTS

Histological Results

The extents of the cortical injuries for Groups TTC and TTD along with their original learning scores are presented in Figs. 1 and 2 respectively. Although not presented, the extents of the injuries in Groups NTC and NTD were very similar in location and scope. The ablations were intended to encompass the area of the temporal neocortex as defined by Horel and Stelzner (1981). Evaluations of the extents and placements of the cortical injuries revealed that those zones were not completely destroyed. The most anterior regions of the temporal neocortex remained intact. In addition, the ablations extended dorsally beyond the zones of the temporal neocortex.

The brains of 18 subjects were further examined for the existence of any subcortical damage. For two of the subjects, the injuries unilaterally nicked the hippocampus and for ten of the subjects, the injuries encroached upon the corpus callosum. Examinations of the dorsal thalamus revealed no signs of degeneration in nucleus dorsomedialis and the dorsal lateral geniculate nucleus. Also, no degeneration was detected in the nucleus lateralis posterior (NLP) despite the fact that Hughes (1977) has demonstrated autoradiographically that NLP sends projections to the area destroyed. The temporal neocortex may receive sustaining projections from NLP,
Fig. 1. The extents of the cortical injuries and the individual original learning scores for Group TTC.
Fig. 2. The extents of the cortical injuries and the individual original learning scores for Group TTD.
and thus when destroyed, results in no degenerative changes in the thalamic nucleus (Rose and Woolsey, 1958). As expected, the lesions encroached upon the auditory cortex which resulted in extensive bilateral degeneration in nucleus marginalis and sparse bilateral degeneration in nucleus centralis of the medial geniculate bodies.

Behavioral Results

The performances of several of the animals in the study were grossly aberrant. An animal was withdrawn from the analysis if its score for original learning was greater or less than two standard deviations away from the mean calculated from all subjects in the group. Of the 72 subjects in the study, 6 subjects met this criterion, and happily, one animal in each group.

In Table 1, the means and standard errors of the means are presented for all the groups in all three phases of the experiment. A 3 x 2 x 3 analysis of variance was performed on the data. Both between-subject factors, surgical condition and condition of contiguity were significant ($F(2, 120) = 13.1, p < .001; F(1, 120) = 11.9, p < .001$). The within-subjects factor, training, was also significant ($F(2, 120) = 105.1, p < .001$). All of the interactions between the factors were significant: Lesion x Contiguity ($F(2, 120) = 14.0, p < .001$; Lesion x Training ($F(4, 120) = 7.0, p < .001$); Contiguity x Training ($F(2, 120) = 16.1, p < .001$); Lesion x Contiguity x Training ($F(4, 120) = 13.4, p < .001$).
Table 1. Means and standard errors of the means for all groups.

<table>
<thead>
<tr>
<th>GROUP</th>
<th>N</th>
<th>SURG</th>
<th>ORIGINAL TRAINING</th>
<th>CONTIGUITY REVERSAL</th>
<th>SURG RETENTION TEST</th>
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<tr>
<td>NNC</td>
<td>11</td>
<td>—</td>
<td>53 ± 8</td>
<td>31 ± 13</td>
<td>—</td>
</tr>
<tr>
<td>NTC</td>
<td>11</td>
<td>—</td>
<td>64 ± 6</td>
<td>11 ± 4</td>
<td>T</td>
</tr>
<tr>
<td>TTC</td>
<td>11</td>
<td>T</td>
<td>48 ± 12</td>
<td>32 ± 11</td>
<td>—</td>
</tr>
<tr>
<td>NND</td>
<td>11</td>
<td>—</td>
<td>59 ± 7</td>
<td>12 ± 3</td>
<td>—</td>
</tr>
<tr>
<td>NTD</td>
<td>11</td>
<td>—</td>
<td>60 ± 8</td>
<td>15 ± 6</td>
<td>T</td>
</tr>
<tr>
<td>TTD</td>
<td>11</td>
<td>T</td>
<td>174 ± 11</td>
<td>29 ± 9</td>
<td>—</td>
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</table>
Post-hoc comparisons were made using the Dunn test for multiple comparisons (alpha = .01). In Phase I, the animals were trained on the plus-square problem either in the contiguous or discontiguous conditions. There were no significant differences among the groups in the contiguous condition. In the discontiguous condition, Groups NND and NTD also did not differ. However, Group TTD was significantly different from both groups NND and NTD. Comparisons were also made between contiguous and discontiguous conditions in each surgical group. Only Groups TTC and TTD significantly differed.

In Phase II, the subjects were trained on the same problem but the condition of contiguity was reversed. The groups were not significantly different from each other. However, all groups except Group NNC showed significant savings when their scores are compared with their original learning scores.

In Phase III, the animals were trained on the same problem under the condition of contiguity trained in Phase I. The performance of the groups were not significantly different from one another. However, the performance of each group when compared to their original learning performance demonstrated significant savings for all of the groups.
DISCUSSION

It is clear from the results of this investigation that injuries to the temporal cortex of rats result in severe impairments of performance of a visual-pattern problem if, and only if, the cues are presented in positions that are discontiguous from the animals' responses. The findings closely parallel results obtained in studies of monkeys with bitemporal injuries, and show that the impairments are impairments of attending rather than impairments of "complex visual processing." Thus, if visual patterns are presented in a manner such that attending to the relevant cues is guaranteed, neither bitemporal rats nor bitemporal monkeys have any difficulty in learning to discriminate between pairs of complex visual patterns.

The fact that temporal rats have no impairments of postoperative learning of the spatially contiguous plus-square problem should put to rest the concept that pattern perception is explicitly dependent upon the integrity of the temporal cortex, and primarily upon the posterior sectors of the regions. In the present study, the zones described by Horel and Stelzner (1981) were not quite completely destroyed; instead, the foci of the injuries were in the region of the posterior temporal cortex. But the injuries were nonetheless sufficient to induce a three-fold difference in the trials required for original learning of the problem when the cues were displaced from the bottoms.
to the tops of small plaques. That shows how powerful the variable can be when animals have temporal injuries, and supports the interpretations of Meyer and Meyer (1982) of the findings for monkeys in the studies of Mishkin and Pribram (1954) and of Ungerleider and Pribram (1977). Again, in those studies, the problems that were found to be difficult for temporal animals to learn were problems in which the differential cues, whether patterns or objects, were displayed on plaques and the animals responded to the edges of the plaques.

It should also be noticed that in this investigation, the performances of normal rats were much the same regardless of whether the cues were presented at the tops or the bottoms of the doors. That could seem at first glance to be inconsistent with outcomes of Cloud, Meyer, and Meyer (in preparation). However, in that investigation, the black and white stripe cues occupied the bottom or top one-quarters of the doors, and in the present study the plus and square patterns occupied the top and bottom halves of the doors. Although such very small differences could seem to matter very little to a rat, there is ample evidence from studies of both normal monkeys and normal rats that they do (Ehrenfreund, 1948; Lashley, 1938; Meyer et al., 1966).

The results of Phase II show that once a normal or temporal rat has learned what stimulus features to attend to, making the stimuli spatially discontiguous has little effect upon performance. These findings are consistent with the results of Schrier and Harlow (1957) with normal monkeys and the results of Butter and Hirtzel (1970) with
inferotemporal monkeys. Thus, the data suggest that the focus of 
attention of temporal rats and monkeys can still be directed toward 
spatially discontiguous areas if the subjects already know what 
stimulus features are relevant to the solution of the problem.

The results of the retention tests in Phase III show that 
temporal rats that have had extensive training on both the S-R 
contiguous and discontiguous tasks before the injuries are inflicted 
have no difficulty with the discontiguous problem when tested for 
retention after surgery. The finding has a parallel in studies of 
bitemporal monkeys, who do much better on discontiguous problems if 
prior to the surgery, they have been given contiguous and 
discontiguous training on the problem (Meyer, 1972). These results 
contrast with findings for temporal monkeys by Iwai and Miskkin (1969) 
and Mishkin and Pribram (1954), who found that their animals had 
impairments of postoperative retention of the plus-square problem. 
However, the animals in those investigations were not 
preoperatively-trained on both a contiguous and discontiguous version 
of the problem. Temporal rats in the present study had previously 
been trained to search for the relevant cues in both contiguity 
conditions. Their habits for doing that apparently survived the 
temporal injuries and negated the effects which are noted when naive 
temporal rats are trained on the problem.

The fact that the "engram" for the solution of the plus-square 
problem survived the temporal ablations and that preoperatively-naive 
temporal rats can solve the spatially contiguous problem, suggests
that the temporal neocortex has little to do with the storage of complex visual memories. Instead, the results of this investigation clearly demonstrate that animals following temporal cortical injuries have a constricted focus of attention. Moreover, this effect is hardly trivial, for a change in the spatial position of the relevant cues of only a few centimeters can produce enormous effects.
LIST OF REFERENCES


