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The Effectiveness of Pattern Homogeneity as a Cue in Subcortical Pattern Vision

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THE EFFECTIVENESS OF PATTERN HOMOGENEITY

AS A CUE IN SUBCORTICAL PATTERN VISION

by

David Strachan

A Thesis Submitted to the Faculty of the Graduate School of Loyola University of Chicago in Partial Fulfillment of the Requirements for the Degree of Master of Arts

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VITA

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGMENTS</td>
<td>ii</td>
</tr>
<tr>
<td>VITA</td>
<td>iii</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>v</td>
</tr>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>LITERATURE REVIEW OF THE EFFECT OF CORtICAL ABATIONS ON THE PERFORMANCE OF DISCRIMINATIONS OF PATTERN</td>
<td>4</td>
</tr>
<tr>
<td>THE PRESENT EXPERIMENT</td>
<td>14</td>
</tr>
<tr>
<td>METHOD</td>
<td>19</td>
</tr>
<tr>
<td>Subjects</td>
<td>19</td>
</tr>
<tr>
<td>Apparatus</td>
<td>19</td>
</tr>
<tr>
<td>Stimuli</td>
<td>21</td>
</tr>
<tr>
<td>Procedure</td>
<td>21</td>
</tr>
<tr>
<td>RESULTS</td>
<td>25</td>
</tr>
<tr>
<td>Histological Results</td>
<td>25</td>
</tr>
<tr>
<td>Behavioral Results</td>
<td>27</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>34</td>
</tr>
<tr>
<td>CONCLUSION</td>
<td>42</td>
</tr>
<tr>
<td>REFERENCES</td>
<td>43</td>
</tr>
<tr>
<td>APPENDIX A</td>
<td>50</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Training Apparatus</td>
<td>20</td>
</tr>
<tr>
<td>2.</td>
<td>Stimulus Conditions</td>
<td>22</td>
</tr>
<tr>
<td>3.</td>
<td>Examples of Lashley Diagrams and Corresponding Degeneration in Lateral Geniculate Nucleus for Animals with Complete and Incomplete Lesions</td>
<td>26</td>
</tr>
</tbody>
</table>
INTRODUCTION

Several recent investigations have attempted to test the responses of animals lacking visual cortex to various types of patterned visual stimuli. Specifically, these studies have been aimed at determining the stimulus characteristics, referred to as cues, which mediate the discrimination of patterned visual stimuli by visually decorticated animals. This research further investigated the cues that mediate discriminations between patterns, specifically the sensitivity of visually decorticated rats to the spatial properties of pattern.

The necessity of identifying the cue mediating the discrimination of patterns was first noted by Smith (1934) and later by Kluver (1941). Smith (1934) proposed that research be conducted "to ascertain what factors are involved in visual stimulus patterns producing discriminative responses" (p. 342). He suggested that this be done by modifying selected parts of the visual stimulus and noting the influence on previously learned responses. Kluver (1941) suggested a similar approach. He stated, "The problem is...to determine the properties of various configurations which are or are not effective in influencing the reactions of the animal" (p. 39).

Prior to Smith's and Kluver's approach to the problem, researchers had considered pattern vision to be a unitary trait possessed by some species and not by others (Bingham, 1913, 1914, 1922; Munn & Steinung, 1931; Neet, 1933). Pattern vision was defined as the
capacity to respond to a particular stimulus shape (triangularity, roundedness, etc.), independent of the position of the stimulus in space and the background on which it appeared. Responses to the shape of the stimulus implied the ability to use abstract concepts descriptive of the pattern as the basis for visual discriminations. Smith (1934) noted, however, that even humans rely on the position of a stimulus and its background in distinguishing between patterns, and that complex patterns can be recognized without reference to abstract concepts. Because of this, Smith rejected the early definition of pattern vision and recommended that research focus on determining the cues mediating the discriminative behavior. These latter approaches to the definition of pattern vision have guided research for the last forty years. Though the phrase "pattern vision" continues to be used as a generic term referring to the ability to see or discriminate between patterned stimuli, it no longer connotes the capacity to respond to abstract concepts of shape.

In addition to the problems in defining pattern vision in subhuman species and establishing the research methodology to study it, early researchers also lacked adequate behavioral measures. In order to demonstrate an animal's response to patterned stimuli, it was necessary to train the animal to perform a behavioral task, i.e., either to recognize a particular stimulus or to discriminate between two stimuli. Only after the development of sophisticated instrumentation and training procedures (Kluver, 1933; Lashley, 1930; Thompson, & Bryant, 1955) did behavioral measures accurately reflect
the degree to which animals could discriminate between patterns. As a result, the animal's capacity to discriminate between patterned visual stimuli was frequently underestimated.

Early investigators also lacked the sophisticated techniques necessary to perform discrete lesions and the histological procedures necessary to confirm the extent of cortical lesions. Improvements in these two areas increased the significance of recent research based on behavioral assessment of lesioned animals.

Finally, two factors stimulated the interest of early researchers in the role of the cortex in behavior. First, its location as the exterior surface of the brain provided accessibility in a relatively simple surgical procedure. Second, the differences in cortical structure between species gave rise to hypotheses concerning cortical functions. Initial studies found that extensive lesions of the posterior cortex produced severe deficits in visual behavior, especially the perception of visual patterns. Subsequent studies indicated, however, that visually decorticated subjects were not totally insensitive to patterned stimuli and did respond to certain types of patterned stimuli. Such responses were presumably mediated by subcortical structures.
LITERATURE REVIEW OF THE EFFECT OF CORTICAL ABLATIONS ON THE PERFORMANCE OF DISCRIMINATIONS OF PATTERN

Initial studies consistently reported the failure of posterior-decorticated animals to perform pattern discrimination tasks. Lashley (1930, 1931) and Lashley and Frank (1934) found that lesioned rats could not discriminate between stimuli differing in form (circles, triangles, and squares) unless the stimuli differed in the amount of light they emitted. Similarly, Kluver (1936, 1937) noted that visually decorticated monkeys could only discriminate between forms that differed in luminous flux (i.e., luminance by area). These observations led early researchers to the conclusion that subjects which had sustained ablations of the visual cortex could only discriminate between stimuli that differed in terms of luminous flux.

Smith (1937, 1938) first reported results contradictory to these initial findings. Six visually decorticated cats were able to follow a moving hand in front of their eyes and exhibited "forced lateral deviations of the eyes" (optokinetic nystagmus) in response to the movement of striped patterns across their visual field (Smith, 1937). In a succeeding study (Smith, 1938), visually decorticated cats retained a high degree of visual acuity and discriminated between horizontal and vertical bars. Smith's results demonstrated that visually decorticated cats could respond to certain characteristics of patterned stimuli.

Kluver (1941) provided additional evidence that visually decorticated subjects could discriminate between patterned stimuli.
In an extensive study, the occipital lobes were removed from two rhesus monkeys which were then trained to discriminate between several patterned stimulus configurations. Though the stimuli were equal in terms of luminous flux, one subject discriminated between a square and either a horizontal or vertical bar. The animal was also able to discriminate between two types of stimuli that differed in the spatial distributions of light: a 38 cm² square versus 76 circles, each .5 cm², spread over a 152 cm² field, and a 38 cm² square versus 4 squares, each 9.5 cm² in the corners of a 152 cm² field. The results indicated that visually decorticated subjects could discriminate between many (though not all) patterned stimuli, and emphasized the need to determine the cues that mediate pattern discrimination.

During the early 1940's, interest in the problem was renewed by Weisærantz's (1963) investigation of a striate-lesioned rhesus monkey. This study tested the discriminative responses of the subject to 11 pairs of patterned stimuli in order to determine which stimulus properties provided the discriminative cues. It was found that the subject could consistently discriminate between those stimuli that differed in amount of contour (i.e., the edge between pattern and background). For example, the subject was able to discriminate between white stripes and a random arrangement of small white rectangles of equal total area, each on a black background. The stimuli emitted equal amounts of luminous flux, but differed in amount of contour.

At the same time, studies that employed stimuli lacking the contour cue generally were unable to obtain discriminative responses
icht all visual cortex had been removed could not discriminate among circles, triangles, or diamond shapes, although subjects with extra-striate visual cortex could do so. Meyer (1963) and Wetzel, Thompson, Horel, and Meyer (1965) were unable to train cats which had undergone extensive bilateral posterior decortication to discriminate between striped and checked patterns. Similarly, Horel, Bettinger, Royce, and Meyer (1966) and Thompson (1970) were unable to train visually decorticated rats to discriminate between lines differing in slope. These results were often interpreted as indicating that visually decorticated subjects could not discriminate between patterns. More accurately stated, the results indicated that visually decorticated subjects were unable to respond to the cues present in these stimuli.

In those studies in which visually decorticated subjects were successfully trained to discriminate between patterned stimuli, controversy occasionally arose as to whether the discrimination was actually based on local brightness cues rather than pattern cues. The capacity of visually decorticated subjects to discriminate between stimuli that differ in luminance has frequently been demonstrated (Lashley, 1930, 1935) and such differences often occurred between sections of patterned stimuli. For example, Winans (1967) trained two visually decorticated cats to discriminate between an upright and inverted triangle—stimuli equated in terms of luminous flux, but which differed with respect to the luminance emitted in either the top or the bottom halves of the stimuli. Dodwell and Freedman (1968) criticized the study, stating
that the discrimination may have been mediated by selective responding to the local brightness differences in the stimuli and that such a discrimination would not constitute a response to pattern. Winans (1968) replied that further research was required to determine the discriminative cue and to ascertain whether the same cue was used by both normal and visually decorticated animals. Subsequent research (Winans, 1971) indicated that local brightness differences contributed to pattern discrimination in both normal and visually decorticated cats. In this study, both normal and lesioned cats were trained to discriminate between upright and inverted triangles and then transferred to modified stimuli. Discrimination performance was disrupted in both groups by the transfer to tasks in which the figure-ground relationship was reversed and tasks in which the triangles were placed in novel positions. These transfers resulted in a change in the brightness gradients of the stimuli. In spite of this evidence for the role of brightness differences in pattern discrimination in normal subjects, brightness differences have not been considered to be pattern cues. Consistent with the argument presented by Dodwell and Freedman (1968), brightness differences generally have not been thought to reflect a particular property of the pattern, but rather a way in which patterns can be discriminated using luminous flux cues. Because of this, more recent studies have employed stimuli designed to eliminate local brightness differences and to test the subject's ability to use characteristics of the pattern to mediate discrimination.

The importance of controlling local brightness differences was
further emphasized by Spear and Braun (1969). Three visually decorticated cats were trained to discriminate between 18 horizontal and 12 vertical stripes. By alternately covering portions of the stimuli, it was found that subjects selectively responded to the bottom half of the stimulus (near the point of reinforcement). In this case, however, no gross brightness differences existed between the stimuli. Instead, it was suggested that the discrimination may have been mediated by differences in the optokinetic reflex to the horizontal and vertical lines. In addition, the authors emphasized the importance of an extended training period (2-10 times preoperative), and the illumination and contrast of the stimuli in training pattern discriminations in visually decorticated subjects.

Wetzel (1969) attempted to determine the cues used by visually decorticated cats in distinguishing between depths on a visual cliff by studying the subject's ability to learn several related visual discrimination tasks. As in previous studies (Meyer, 1963; Wetzel et al., 1965), the lesioned subjects failed to discriminate between checked and striped stimuli. They did, however, learn to discriminate between near and distant checked stimuli, between near and simulated distant (two dimensional projection) checked stimuli, and between large and small checks. The results suggested that contour differences between the stimuli may have mediated the discrimination. Using stimuli similar to Wetzel (1969), Braun, Lundy, and McCarthy (1970) varied flux differences, visual perspective, and local brightness cues to determine which of these cues mediate discrimination between near and distant stimuli.
in visually decorticated rats. It was found that lesioned subjects could discriminate between checked patterns at different distances equated on all three of these characteristics. The subjects were unable to discriminate between stimuli that differed only with respect to the brightnesses emitted by stimuli at different distances, or between horizontal and vertical stripes. The results demonstrated that visually decorticated rats could discriminate between patterns, though the authors did not identify the cue or cues that mediated the discrimination.

During this same period, several studies reported results supporting the effectiveness of amount of contour as a cue for visually decorticated subjects. Lewellyn, Lowes, and Isaacson (1969) trained visually decorticated rats to discriminate between the numerals '5' and '0', stimuli that were equal in luminous flux but different in amount of contour. A study by Mize, Wetzel, and Thompson (1970) was designed to provide a more rigorous test of the effectiveness of contour as a pattern cue. Visually decorticated rats were trained to discriminate between two large triangles and either 13, 32, or 50 smaller ones, resulting in contour ratios of 3:1, 4:1, and 5:1, respectively. The stimulus with the greatest contour ratio was learned in the least number of trials and the one with the lowest contour ratio required the greatest number of trials. The results supported the effectiveness of contour as a pattern cue in visually decorticated animals.

Dalby, Meyer, and Meyer (1970) also reported evidence indicating the effectiveness of contour as a pattern cue. In this study, seven
cats with extensive visual cortical lesions (three subjects sustained almost complete removal of visual cortex) were trained to discriminate between a checked pattern and a series of other stimuli: vertical stripes, horizontal stripes, smaller checks, large circles, and small circles. The stimulus pairs were categorized according to whether they differed in amount of contour or the number of corners contained in the patterns. Stimuli differing in the amount of contour were readily discriminated, though the results concerning the role of corners as a cue were equivocal. The authors suggested that an additional cue may have contributed to the discrimination of several stimulus pairs. The fact that the discrimination between large circles and large squares (stimuli equal in contour) was quickly learned suggested that the difference in visual subspace (i.e., the difference in the number of black and white spaces) may have been an effective cue. The authors hypothesized that visually decorticated subjects could tell when a space was filled with objects, and yet not recognize the shapes of those objects. The effectiveness of this cue, however, has not been directly tested.

Additional evidence for the effectiveness of the contour cue was provided by Cowey and Weiskrantz (1971). Seven rats underwent striate cortical ablations (some lesions appeared to include the entire visual area) and were trained to discriminate between either moving or stationary stripes and a grey stimulus of equal luminosity. Although the conclusions must be guarded due to the limited extent of the lesions, the study is consistent with others supporting contour
as a pattern cue for visually decorticated animals.

Several recent studies have investigated the capacity of visually decorticated animals to discriminate between geometric patterns. In general, these studies have reported an inability to train lesioned subjects to discriminate between geometric figures equated in terms of local luminance. Pasik and Pasik (1971) and Schilder, Pasik, and Pasik (1972) found that visually decorticated monkeys could discriminate between a circle and a triangle only when the lesions were incomplete and spared nonstriate visual areas. Likewise, Doty (1971) reported that striate lesioned cats could discriminate between figures, but that cats which had undergone complete visual-cortical lesions could not. These studies support the earlier conclusions by Lashley (1930), and Lashley and Frank (1934), and Kluver (1941) that visually decorticated subjects could not discriminate between stimuli that differ only in the shape of the pattern.

In sum, many of the results of recent research have suggested that animals deprived of visual cortex retained the capacity to respond to certain types of patterned stimuli. Lesioned subjects retained the optokinetic reflex to moving vertical lines (Smith, 1937, 1938), which Spear and Braun (1969) suggested may also mediate the discrimination of some stationary patterns. Lesioned subjects could also discriminate between stimuli on the basis of contour differences (Cowey & Weiskrantz, 1971; Dalby et al., 1970; Lewellyn et al., 1969; Mize et al., 1971; Weiskrantz, 1963; Wetzel, 1969). Visually decorticated subjects appeared, however, to be unable to discriminate between shapes (Doty,
1961, 1971; Pasik & Pasik, 1971; Schilder et al., 1972) or between lines that differed in slope (Lashley and Frank, 1934).

Recent results also suggested that successful discrimination may require special training conditions. The need for extended training periods, up to ten times the number of preoperative trials, was mentioned frequently (Cowey & Weiskrantz, 1971; Lewellyn et al., 1969; Spear & Braun, 1969; Winans, 1967, 1971). In addition, it was necessary that patterns be brightly illuminated, possess high contrast, and be fairly large with respect to the animal's visual field (Cowey & Weiskrantz, 1971; Spear & Braun, 1969).

Finally, recent research also revealed the need for complete and accurate lesions in studies demonstrating pattern vision in visually decorticated subjects. Lashley (1939) concluded that the sparing of small areas of visual cortex may result in near normal cortical functioning. This finding, in addition to those of Doty (1961, 1971), suggested that the functioning organization of the cortex may be quite divergent, that small portions of any area of the visual cortex may be able to perform certain functions as well as the entire cortex. This conception of the functional organization of the cortex received support from studies by Lewellyn et al. (1969), Mize et al. (1971), and Spear and Braun (1969), in which the lesion size was found not to be related to performance on pattern discrimination tasks. In addition, other studies have indicated that the extent of the lesion must be limited to visual cortex to avoid damage to subcortical centers that may function in the discrimination of patterns when the cortex has been
removed. Research has also indicated that unnecessary damage to the cortex beyond the visual area may disrupt discrimination in ways unrelated to visual processes and must be avoided.
THE PRESENT EXPERIMENT

A comparison of the studies in which visually decorticated animals have discriminated between patterned stimuli and those in which they have not suggested an alternative and more parsimonious explanation of the visual abilities of visually decorticated animals. Most of the discriminable stimuli differed not only in terms of the cues just discussed, but also in terms of the spatial distribution of the pattern across the stimulus, a cue which will be referred to as "pattern homogeneity." Pattern homogeneity is defined as the degree to which pattern and background are equally distributed in each portion of the stimulus. Those stimuli that were not discriminable did not appear to differ in this respect. Other studies have proposed the potential significance of cues of this type, though the cue has not been formally defined previously. Kluver (1941), for example, postulated that the "spatial distribution of light" may have mediated the discrimination of one circle (low homogeneity) versus seventy-six smaller circles (high homogeneity) by a visually decorticated monkey. Pattern homogeneity is also similar to the concept of visual subspace proposed by Dalby et al. (1970). It differs from visual subspace in its emphasis on the apportionment of the patterned area rather than the number of forms, though the cues may be functionally equivalent.

Among those studies in which visually decorticated subjects have successfully discriminated between patterned stimuli, contour was often mentioned as the relevant cue. These studies frequently employed stimuli that differed in the number of objects they contained (one or
(one or two large shapes versus many small ones) and, consequently, in the amount of contour they contain (Cowey & Weiskrantz, 1971; Kluver, 1941; Mize et al., 1971; Weiskrantz, 1963). However, the contrast between the stimuli in the number of objects they contained also resulted in differences between the stimuli in the amount of area covered by the patterns. Thus, the cues of contour and pattern homogeneity were often confounded in these stimuli.

Stimuli consisting of checked patterns that differed in the number and size of the squares have also been used to demonstrate the effectiveness of contour as a cue (Dalby et al., 1970; Wetzel, 1969). As in the previously described stimuli, these checkerboard patterns also differed with respect to both pattern homogeneity and contour, and either or both of the cues may have mediated the discrimination.

A review of those stimuli that visually decorticated subjects failed to discriminate shows that most of the stimuli did not differ in terms of pattern homogeneity, though they exhibited other cues. Visually decorticated animals failed, for example, to discriminate between lines differing in slope in a large number of studies (Braun et al., 1970; Horel et al., 1966; Lashley, 1930; Thompson, 1970). In the two exceptions in which lesioned subjects did discriminate between these stimuli (Smith, 1938; Spear & Braun, 1969) additional cues were available. The stimuli employed by Smith (1938) resulted in local brightness differences of the type discussed by Winans (1971). In Spear and Braun (1969), the horizontal and vertical stimuli differed
not only in slope, but also in number, thus confounding slope with pattern homogeneity.

Visually decorticated subjects also failed to discriminate among geometric shapes (Doty, 1961, 1971; Kluver, 1941; Lashley & Frank, 1934; Schilder et al., 1972). Again, stimuli of these types were often similar in pattern homogeneity.

In each of the preceding studies in which visually decorticated subjects discriminated between patterned stimuli, both pattern homogeneity and contour have been available as cues. The confounding of the cues made it impossible to determine which one was mediating the discrimination, or whether successful discrimination required both cues.

Some evidence suggested that pattern homogeneity may be the more important of the cues, and that it, by itself, may be sufficient to mediate discrimination. First, Schilder et al. (1971) reported that a posterior-decorticated monkey performed a pattern discrimination on the basis of brightness cues, rather than an available contour cue. Similarly, visually decorticated subjects have consistently been unable to discriminate between checked and striped patterns (Meyer, 1963; Wetzel et al., 1965; Wetzel, 1969), even though these patterns do differ in amount of contour. These results suggested that contour alone may be insufficient to mediate pattern discrimination in visually decorticated animals.

Secondly, Dalby et al. (1970) reported that visually decorticated cats exceeded chance performance on a discrimination problem in which
the stimuli were equated in terms of contour, but differed in terms of visual subspace (also in terms of pattern homogeneity). This finding, though not conclusive, suggested that pattern homogeneity may mediate pattern discrimination in visually decorticated animals.

Finally, a series of studies (Pasik, Pasik, & Schilder, 1969; Schilder, 1966; Schilder et al., 1971) provided indirect support for pattern homogeneity as an independent cue. These studies demonstrated the ability of posterior-decorticated subjects to discriminate between stimuli equated for luminous flux but differing in area and luminance. A "photocell" theory was proposed that suggested the subjects' head movements result in different rates of change in luminous flux, mediating a discriminative response. In an analogous manner, head movements would result in different rates of change for stimuli that differ in pattern homogeneity. In this way, visually decorticated subjects could respond to contour-equated stimuli on the basis of differences in pattern homogeneity.

To summarize, a review of the literature revealed that in those studies in which visually decorticated subjects have discriminated between patterned stimuli, both pattern homogeneity and contour cues have been available. Additional evidence suggested that pattern homogeneity rather than contour may have been the critical cue.

In order to determine the relative contributions of contour and pattern homogeneity cues to the performance of pattern discrimination by visually decorticated animals, the following experiment was performed. Visually decorticated rats were trained to discriminate
between stimuli in which only one or the other of the two cues were present. Superior performance on the part of subjects trained on one or the other of the stimuli indicated the relative effectiveness of the cues. In a similar manner, subjects were trained to discriminate between stimuli in which both of the cues were present. When this task was learned, subjects were transferred to stimuli containing only the contour or the pattern homogeneity cue, in order to determine whether either cue alone, or both cues together mediated the discrimination of the stimuli in which the cues had been confounded.
METHOD

Subjects

Thirty-four male, Long-Evans hooded rats, approximately 200 days old at the time of surgery, were used. They were provided with ad lib food and water throughout the course of the experiment. Initially, ten subjects were semirandomly assigned to each of the three training conditions. When examination of the lesions indicated that several animals had received incomplete lesions, four subjects were added to the experiment. One subject was assigned to Condition II and three to Condition III.

Apparatus

Subjects received shock avoidance training in a modified Yerkes apparatus similar to one used by Parker, Erikson, and Triechler (1969) (see Figure 1). Shock was supplied by a Scientific Prototype shock scrambler model 4008j and ranged in intensity from 0 to 20 ma. Stimulus patterns were 4" by 4" photographic copies of drafted designs, mounted between pieces of clear and opaque 1/16" plexiglass. The stimulus cards served as doors between the shock grid and the goal boxes. The doors could be either "activated" or "deactivated." In the activated state the door dropped when the pedal immediately in front of it was depressed, permitting escape from the shock grid into the goal box. In the deactivated state the door was locked, preventing escape from the shock grid. The door containing the positive stimulus was always activated and the other door always
FIGURE 1  TRAINING APPARATUS
deactivated. The stimulus cards were placed in position and reset between trials by hand.

**Stimuli**

Three stimulus conditions were used (see Figure 2). In Condition I, one stimulus card contained two, completely darkened, large circles. The other contained two bull's-eye designs, each consisting of four concentric rings. The stimuli were equal in darkened area and similar in pattern homogeneity, but differed in amount of contour in a 6:1 ratio. In Condition II, the same bull's-eye designs were contrasted with 50 small darkened circles. These stimuli were also equal in darkened area, but differed with respect to both contour (5:1 ratio) and pattern homogeneity. Condition III stimuli consisted of a pair of three ring bull's-eyes versus 18 darkened circles. These stimuli contained equal amounts of darkened area and contour, and differed only in terms of pattern homogeneity. The 18 circles provided a more even distribution of pattern across the stimulus than the concentric rings. The patterns were drawn in black ink on plain white paper and photographed on high contrast Kodalith film.

**Procedure**

*Surgical procedure.* Each subject underwent ablation of visual cortex under asceptic surgical conditions. Under sodium pentobarbital anesthesia, sections of the skull were removed by drill and rongeur, the dura was cut and retracted, and the visual cortex aspirated by pipette. Ten thousand units of penicillin were administered as a postoperative antibiotic and a recovery period of two weeks allowed.
FIGURE 2. STIMULUS CONDITIONS
Training procedure. Following the recovery period, each subject was semirandomly assigned to one of the three previously described conditions. On the first day of training, subjects were acclimated to the equipment for one hour. Under conditions of low shock and dim light, subjects were allowed to explore the apparatus with both goal box doors activated.

On the second day, subjects were trained to avoid shock and corrected for position responding. Shock was administered if the subject did not leave the start box within 5 seconds of the opening of the door and ceased after he had left the start box. If the subject did not enter one of the goal boxes within 20 seconds after leaving the start box, shock was again administered until the subject entered one of the goal boxes. Trials were separated by a 30 second intertrial interval. Training continued until the subject avoided shock on five consecutive trials. If the subject responded to the same goal on the five "avoidance" trials, the door was deactivated and training continued until the subject responded to the other door for five consecutive errorless trials. An error occurred when the subject depressed the pedal in front of the negative (deactivated) stimulus door or placed his paws directly on the door. Errors were punished by the administration of a brief shock.

On the third day, subjects were trained to discriminate between black and white stimuli. One of the stimuli was randomly assigned as the positive stimulus for each subject. Training continued until the subject achieved a criterion of 18 out of 20 correct trials.
Finally, subjects were semirandomly assigned to each stimulus condition and trained to a criterion of 18 out of 20 correct trials. Training was conducted in two 25-trial sessions per day, separated by at least two hours. According to a predetermined random schedule, the subject was presented one of eight stimulus arrangements that differed with respect to the rotation of each stimulus and the position of the positive stimulus in either the right or left goal box. This prevented performance of the discrimination on the basis of local brightness cues or responses to position rather than the positive stimulus. Each stimulus served as the positive stimulus for half of the subjects in that condition. Training was terminated if the criterion had not been met after 750 trials.

Upon attainment of criterion, subjects in Condition II participated in a transfer condition; they were semirandomly assigned to either Condition I or Condition III and trained to criterion under that condition. Because subjects in Condition II had been trained to respond to both contour and pattern homogeneity as either positive or negative cues, assignment to the transfer task was consistent with their previous training.

Histological procedure. At the conclusion of the experiment, each subject was put under deep anesthesia and perfused through the heart with a formal saline solution. The brains were removed from the skulls and the extent of the lesions recorded on Lashley diagrams. Finally, the brains were embedded in celloidin, sectioned at 20μ, and stained with thionin to determine the amount of degeneration in the lateral geniculate nucleus.
RESULTS

Histological Results

After the brains had been histologically prepared, each was examined using a light microscope at high magnification (400x). Animals were categorized as having received complete or incomplete lesions based on the extent of degeneration in the dorsal portion of the lateral geniculate nucleus.

The criteria established by Lashley (1934, 1939) were used to identify the degeneration resulting from a visual cortical lesion. Changes indicative of degeneration included local cell loss, atrophy of the remaining cells, and gliosis. A complete lesion was defined as total degeneration of the dorsal portion of the lateral geniculate nucleus throughout its anterior-posterior projection. Degeneration of this extent usually results from complete removal of areas 18 and 18a as defined by Kreig (1946). An incomplete lesion was identified by the presence of localized clusters of cells lacking the previously mentioned abnormalities. Examples of the Lashley diagrams and histological material for animals with complete lesions and animals with incomplete lesions are presented in Figure 3.

Examination of the histological material indicated that 18 animals received complete lesions (I = 5, II = 6, III = 7) and 16 animals received incomplete lesions (I = 5, II = 5, III = 6). In most cases in which the lesions were incomplete, clusters of normal cells were found in the dorsal lateral portion of the lateral geniculate nucleus.
Figure 3  Examples of Lashley Diagrams and Corresponding Degeneration in Lateral Geniculate Nucleus for Animals with Complete and Incomplete Lesions
geniculate nucleus, indicating that the posterior medial portion of the visual cortex had been left intact.

Behavioral Results

Comparisons were made among the three stimulus conditions. The data presented are the number of trials required by animals in each of the discrimination conditions to reach a criterion of 18 out of 20 correct trials. The results are summarized in Table 1. The means, medians, and standard deviations are presented for animals in each of the three stimulus conditions and for the animals transferred from Condition II to Conditions I and III.

Results for animals with complete visual cortical lesions are shown separate from those with incomplete lesions. This distinction is demanded by the results of several studies (e.g., Lashley, 1939) that demonstrated that even small remnants of visual cortex are sufficient to mediate the discrimination of patterns which differ in shape. Animals with complete lesions, however, required many more trials, and frequently failed to discriminate between similar stimuli. The differences in performance suggested that visual discrimination in animals with incomplete lesions may differ qualitatively from discrimination performance among animals with complete lesions. Therefore, it would not be appropriate to combine the results for these two groups of animals. The results for animals with complete lesions will be reported first.

The performance of animals in the three stimulus conditions indicated that rats with complete visual cortical lesions can dis-
Table 1

Number of Trials to Criterion for Animals in each Stimulus Condition

**Complete Lesions**

<table>
<thead>
<tr>
<th>Stimulus Condition</th>
<th>n</th>
<th>Mean</th>
<th>Median</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>5</td>
<td>536.60</td>
<td>700.00</td>
<td>228.84</td>
</tr>
<tr>
<td>II</td>
<td>6</td>
<td>317.17</td>
<td>298.00</td>
<td>218.78</td>
</tr>
<tr>
<td>III</td>
<td>7</td>
<td>269.00</td>
<td>168.00</td>
<td>189.63</td>
</tr>
<tr>
<td>transferred to I</td>
<td>2</td>
<td>90.00</td>
<td>90.00</td>
<td>39.00</td>
</tr>
<tr>
<td>transferred to III</td>
<td>2</td>
<td>61.50</td>
<td>61.50</td>
<td>39.50</td>
</tr>
</tbody>
</table>

**Incomplete Lesions**

<table>
<thead>
<tr>
<th>Stimulus Condition</th>
<th>n</th>
<th>Mean</th>
<th>Median</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>5</td>
<td>323.40</td>
<td>355.00</td>
<td>225.76</td>
</tr>
<tr>
<td>II</td>
<td>5</td>
<td>302.00</td>
<td>306.00</td>
<td>133.81</td>
</tr>
<tr>
<td>III</td>
<td>6</td>
<td>222.17</td>
<td>157.00</td>
<td>241.72</td>
</tr>
<tr>
<td>transferred to I</td>
<td>2</td>
<td>221.50</td>
<td>221.50</td>
<td>123.50</td>
</tr>
<tr>
<td>transferred to III</td>
<td>2</td>
<td>149.50</td>
<td>149.50</td>
<td>8.50</td>
</tr>
</tbody>
</table>
criminate between stimuli that differ in terms of either contour (Condition I), pattern homogeneity (Condition III), or both (Condition II). Six of the seven animals in Condition III (pattern homogeneity) achieved the criterion. The median number of trials was 168. In Condition II, which contained both the pattern homogeneity and contour cues, five of the six animals achieved the criterion. The median number of trials required was 298. In Condition I, which contained the contour cue, only two of the five animals in the group achieved the criterion. The median number of trials required was 700.

A Kruskal-Wallis non-parametric analysis of variance was performed to determine whether significant differences existed among the three stimulus conditions. No significant differences were found between the number of trials necessary to reach the criterion ($H = 2.81, p < .25$). However when comparisons between conditions were tested by Fisher's exact test, marginally significant differences were found between Condition I (contour cue) and the other two conditions: $I > III, p < .11; I > II, p < .10$. In other words, stimuli that differed in amount of pattern homogeneity (Condition III) or both pattern homogeneity and contour (Condition II) were discriminated in fewer trials than stimuli that differed only in amount of contour (Condition I).

The difference in trials to criterion between animals transferred from Condition II to Condition I and those transferred to Condition III also supported the conclusion that contour alone is not as effective a cue as pattern homogeneity in the mediation of pattern
discrimination. Animals transferred from Condition II to Condition I required an average of 90 trials to reach criterion and those transferred to Condition III required an average of 61.5 trials. Although the difference between the number of trials to criterion for the two groups was not statistically significant, \( t(2) = .51, p < .25 \), the direction of these results was consistent with the comparison between animals trained on Condition I and Condition III without previous experience on Condition II.

Results for animals with incomplete lesions differed from the results for animals with complete lesions in several respects. First, although the difference was not statistically significant, animals with incomplete lesions required fewer trials to reach criterion than animals which had sustained complete lesions. Second, unlike animals with complete lesions, no significant or marginally significant difference existed among the stimulus conditions for animals with incomplete lesions. Third, considerably less positive transfer was found from Condition II to Conditions I and III among animals with incomplete lesions (Condition I, \( \bar{M} = 221.5 \); Condition III, \( \bar{M} = 149.5 \)), though again the difference was not statistically significant \( t(6) = 1.83, p < .20 \). In general, however, the results for animals with incomplete lesions were in the same direction as those with the complete lesions.

The stimulus pairs presented to animals in each condition differed not only with respect to the cues they contained, but also in terms of three other stimulus characteristics. First, the orientation of the
stimuli was randomly varied from trial to trial to prevent performance of the discrimination on the basis of local brightness cues. Secondly, the location of the positive stimulus on the left or right side was also randomly varied to prevent the mediation of the discrimination by the location of the positive stimulus. Finally, half of the animals in each condition were trained with each stimulus as the positive stimulus to reduce any effect of this variable. Although the three stimulus conditions were equated for these variations in stimulus presentation, a second analysis was performed to determine whether either of the variables interacted significantly with the three experimental conditions. The percent correct was computed for each animal on each of the 16 types of stimulus presentations (2 positive stimuli × 2 positive stimulus positions × 4 stimulus orientations) within each stimulus condition. Although the types of presentations differed in terms of the number of times they appeared, the percent correct data indicated whether particular types of presentations were consistently discriminated correctly. Such a finding for a particular type of stimulus presentation would suggest that it had been mastered early in the course of training, and may have contributed disproportionately to the attainment of the criterion.

These data were analyzed in a three-factor analysis of variance comparing stimulus conditions (three types of cues) × positive stimulus (two stimuli) × stimulus variations (4 orientations × 2 locations of the positive stimulus). Each factor was considered to be fixed, the first two accounting for between-subjects variation and the third contributing to
within-subjects variation. Among subjects with complete lesions, the analysis resulted in no significant main effects or interactions. Therefore, no type or types of stimulus presentations were significantly more effective than the others in mediating the discrimination between stimuli.

A similar analysis among subjects which had sustained incomplete lesions resulted in a significant main effect for stimulus variation ($F(14, 182) = 7.92, p < .01$) and a significant interaction between condition, positive stimulus, and stimulus variation ($F(14, 182) = 3.45, p < .01$). In addition, a marginally significant interaction was found between a stimulus condition and stimulus variation ($F(14, 182) = 1.67, p < .10$). A comparison among the eight levels of the stimulus variation factor indicated that the significant main effect was largely due to the difference between the presentation of the positive stimulus on the left versus the right side. Stimulus variations in which the positive stimulus was located on the left side were responded to correctly 70% of the time, but those on the right side received only 50% correct responses. This difference apparently reflects the tendency of a number of animals to respond only to one side, irrespective of the stimulus displayed on the door. This type of strategy, called "position responding," was found to be positively correlated to the amount by which the lesion size in the left hemisphere exceeded that in the right hemisphere ($\rho = .34$), as determined by procedures described in Appendix A.
Examination of the Stimulus Condition X Positive Stimulus X Stimulus Variation interaction revealed that the tendency for animals to position respond to the left was greater in Condition I and Condition II among animals trained to go to the low contour or low contour-low pattern homogeneity stimulus, but greater in Condition III among subjects trained with the high pattern homogeneity stimulus as the positive stimulus. The marginally significant interaction between condition and stimulus variation resulted from a slightly greater tendency among animals in Condition III than in Conditions I and II to respond to the left stimulus.
DISCUSSION

The performance of animals in Conditions I and III demonstrated that visually decorticated rats could discriminate between patterned stimuli of equal luminosity but which differed in terms of either contour or pattern homogeneity. Forty percent of the animals in Condition I and 86% of the animals in Condition III achieved the criterion.

In addition, a comparison of the number of trials required to achieve the criterion in Conditions I and III suggested that differences in pattern homogeneity may have provided a more effective cue than contour difference. It was found that animals in Condition III learned to discriminate in fewer trials than animals in Condition I, and that animals transferred from Condition II to Condition III learned faster than animals transferred to Condition I. Also, animals trained on both contour and pattern homogeneity cues (Condition II) performed no better than animals which received only the pattern homogeneity cue (Condition III), suggesting that the contour cue contributed relatively little to the discrimination in Condition II. The conclusion that pattern homogeneity provided a more effective cue than contour must remain tentative, however, because the differences between Conditions I and III were of only marginal statistical significance and because non-significant differences were found in the transfer task.

The differences in performance between subjects with incomplete lesions and those with complete lesions suggested that different
processes (cortical versus subcortical) may have mediated the discrimination of patterns in these two groups of animals. First, consistent with other studies of discrimination performance (Lashley, 1939; Mize et al., 1971), animals with incomplete lesions required fewer (though not significantly fewer) trials to reach criterion than animals with complete lesions. Secondly, animals with incomplete lesions demonstrated less positive transfer (again, not statistically significant) from Condition II to Conditions I and III than animals with complete lesions, suggesting that experience on Condition II contributed disproportionately to the performance of animals with complete lesions. It may have been the case that animals with complete lesions were sensitive only to specific characteristics of the stimuli (e.g., contour and pattern homogeneity) and, therefore, transferred readily from Condition II to Conditions I and III. Animals with incomplete lesions, however, may have perceived additional characteristics of the stimuli (e.g., number and size of circles) that caused Condition II to appear dissimilar to Conditions I and III and disrupted the transfer between training conditions. The results are consistent with Lashley (1939) and Doty (1961), and support the conclusion that animals with complete lesions differ from those with incomplete lesions in the way in which they process visual stimulation.

Differences found between animals with complete lesions and incomplete lesions with respect to position responding were apparently the result of factors other than the experimental manipulation of the stimuli. The difference in lesion sizes, especially, may have been
related to the tendency to position respond. Among animals with incomplete lesions, tissue was more often spared in the left hemisphere than in the right hemisphere, probably resulting in less impairment of the right eye than the left eye. In responding to the stimuli, animals with incomplete lesions may have selectively used their right eyes, orienting their heads to the left and increasing the likelihood of running in that direction. The positive correlation between position responding and the difference between left and right lesion sizes offered further support for the relationship between position responding and lesion sizes.

Parker and Triechler (1973) suggested a second explanation of the tendency of animals with incomplete lesions to position respond. This study found that removal of anterior extrastriate cortex reduced position responding among rats with visual cortical lesions. It is likely that in the present study, more anterior extrastriate cortex was removed among rats with complete lesions than among rats with incomplete lesions, thus accounting for this difference between the two groups of animals. Parker and Triechler's (1973) findings do not suggest, however, why animals position responded primarily to the left side.

The significant interaction between tendency to position respond, stimulus condition, and positive stimulus was probably influenced both by the disparity between lesions sizes and the small number of animals in each cell of the analysis. Comparisons of the lesion sizes indicated that right hemisphere lesions were larger than left hemisphere
lesions in Conditions II and III, but that little difference existed between lesion sizes among animals in Condition I. Since rats were semirandomly assigned to stimulus conditions after decortication, the difference in lesion sizes and corresponding tendency to position respond was apparently a random occurrence. The statistical significance of the interaction also appears to have been influenced by the unequal number of animals with incomplete lesions in the stimulus conditions and the small cell frequencies in the analysis. Thus, the statistically significant interaction may not reflect a meaningful difference in the discrimination performance of animals as a result of different stimulus conditions.

In interpreting the results of the experiment, some consideration must be given to the extreme variability in the number of trials to criterion, as indicated by the standard deviations in Table 1. The degree of variability was not consistent with previous studies of this type (Braun et al., 1970; Mize et al., 1970) and undoubtedly masked the effects of the experimental manipulations. The high variability within each condition made it difficult to demonstrate statistically significant differences among the groups, even when large differences were found among the means and medians. The variability in performance does not appear to have been related to the size or completeness of the lesions—the standard deviations for animals with complete lesions were similar to those with incomplete lesions. The high variability may have been related, however, to the type of response required of the animal in order to escape from shock. Entrance to the goal box could be secured
only by depressing the pedal in front of the positive stimulus and stepping up (over the falling door) into the goal box. Animals appeared to differ greatly in the ways in which they performed this two-part sequence. Animals frequently received no reinforcement (escape from shock) or delayed reinforcement because they had not depressed the pedal, though they had responded to the positive stimulus. The variability may have been reduced had the escape response been closer to natural rat escape-behavior, e.g., running under a stimulus card. The variability may also have been less had more animals been included in the study, but the sizes of the groups were limited by considerations of time and availability of animals.

In general, the results supported the conclusions of previous studies (Dalby et al., 1970; Mize et al., 1971; Weiskrantz, 1963) that subcortical visual structures can mediate discrimination between patterned visual stimuli that differ in amount of contour. In addition, the results suggested that previous studies had confounded the contour and the pattern homogeneity cue, and that pattern homogeneity alone was sufficient to mediate discrimination. Although the results suggested that pattern homogeneity may have been a more effective cue than contour, they did not confirm the speculation that, among studies in which the cues had been confounded, pattern homogeneity rather than contour had been the discriminative cue.

The results of the present study, especially those which indicate the effectiveness of the pattern homogeneity cue, add to the existing information concerning the visual abilities of visually
decorticated animals. In spite of the accumulating evidence that
subcortical structures can mediate the discrimination of patterns,
little is known about the way in which visually decorticated animals
use contour and pattern homogeneity cues. One explanation, proposed
by Weiskrantz (1963), suggested that visually decorticated animals
respond to "the integral of all retinal ganglionic activity." In
other words, the animal is sensitive to transitions between light
and dark, as found in black-white edge, i.e., contour. Weiskrantz's
hypothesis suggests that differences in amount of contour result in
different amounts of stimulation to the animal, thus mediating the
discrimination of patterns that differ in amount of contour.

Although Weiskrantz's explanation does not discuss the effects
of the spatial distribution of the pattern on retinal ganglionic
activity, his model may be expanded to account for a spatial cue.
Several studies (e.g., Hartline, 1940; Kuffler, 1953) have found
that the strength of the retinal ganglionic response was influenced
not only by the amount of contour, but also by its spatial distribution.
These studies demonstrated the effectiveness of lateral inhibition, a
process by which retinal ganglionic activity is inhibited by the
stimulation of surrounding retinal cells. In a similar manner, lateral
inhibition may have reduced the stimulation from low homogeneity stimuli
(e.g., concentric rings in Condition III) in comparison to the high
homogeneity stimuli (e.g., dots in Condition III). Thus, the total
retinal ganglionic activity may be a function of the amount of contour
and its distribution (pattern homogeneity) in the stimulus. Additional
studies comparing the pattern homogeneity cue and the contour cue, and their interaction are required to test this hypothesis.

A second explanation, proposed by Pasik et al. (1969) emphasized the use of rates of change in luminous flux to mediate the discrimination between stimuli. Although the total amount of luminous flux emitted by two stimuli may be equal, the intensity at the eye of the observer will vary with changes in distance between the observer and the stimuli. Pasik et al. (1969) suggested that a visually decorticated animal could discriminate between flux equated stimuli differing in area by moving his head in front of the stimuli and by attending to the different rates of change in luminous flux from the stimuli (cf. p. 16). The same process may also explain the ability of lesioned subjects to discriminate between stimuli equal in area and flux but that differ in the distribution of the luminous flux (pattern homogeneity). Unlike Weiskrantz’s hypothesis, which focused on the amount of contour, the photocell model emphasized the spatial distribution of the pattern. Therefore, it represents a more parsimonious explanation for the effectiveness of the pattern homogeneity cue. The model may also explain the observation of Dalby et al. (1970) that visually decorticated animals could discriminate between figures equated in terms of luminous flux and contour but that differed in terms of visual subspace, another measure of the distribution of pattern.

Additional support for the photocell model may be drawn from the observation that animals in the present study frequently paused in front of the stimuli, moving their heads back and forth in a manner that would
enhance changes in luminous flux differences. Unfortunately, the data recorded was not sufficient to relate the head movements among visually decorticated animals to success in the discrimination of patterns.
CONCLUSION

The results of the study suggested that both contour and pattern homogeneity may be effective cues in the mediation of pattern discrimination in visually decorticated animals. The demonstration of the pattern homogeneity cue was especially important as an indication that the spatial properties of patterned stimuli are effective in the mediation of pattern discrimination. Further research is necessary, however, to generalize the effectiveness of the pattern homogeneity cue to other types of stimulus designs and other species of animals. Also, the mechanisms underlying the discrimination of pattern homogeneity differences in visually decorticated animals must be determined. It is necessary to determine whether pattern homogeneity is simply an adjunct to the contour use, as Weiskrantz's hypothesis might suggest, or whether it constitutes a stimulus dimension to which the subcortical visual centers can respond directly.
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APPENDIX A
In addition to the examination of degeneration in the lateral geniculate nucleus, another measure of lesion size was made. The Lashley diagram for each brain was systematically compared to the Lashley diagram for a rat's brain that had sustained a complete visual cortical lesion (Lashley, 1934) to determine the percent of visual cortex that had not been removed by the surgical operation. The procedure involved projecting the Lashley diagram for the lesioned subject over the diagram of a rat's brain with a complete lesion and computing the percent of visual cortical area not covered by the subject's lesion.

For two reasons, the decision as to whether a particular lesion was complete or incomplete was based solely on the amount of degeneration in the lateral geniculate nucleus. First, because lesioning often killed cortical tissue without removing it (by undercutting and destroying the vascular system), this method provided a conservative estimate of lesion size. Secondly, degeneration in the dorsal portion of the lateral geniculate nucleus is the more widely accepted criterion for a complete visual cortical lesion.

Because no quantified measurement of amount of degeneration was available, it was not possible to obtain a correlation coefficient between the two measures of lesion completeness. It was found, however, that the percent of cortex removed as estimated by the Lashley diagrams was significantly greater for the subjects judged to have complete degeneration of the lateral geniculate nucleus than for those
subjects judged to have incomplete degeneration ($t (30) = 2.13$, $p < .025$). To this extent the two measures agreed on the assessment of lesions as complete or incomplete.

The quantification of the lesion sizes as recorded on the Lashley diagrams was especially useful in the comparison of lesions in the right and left halves of the brain. Analysis of the lesion sizes indicated that lesions of the right visual cortex were generally larger than lesions of the left visual cortex.
The thesis submitted by David D. Strachan has been read and approved by the following Committee.

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Assistant Professor, Psychology, Loyola

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

Date 5-19-75  
Director's Signature