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VISUAL CORTICAL LESIONS IN THE CAT: A STUDY OF DEPTH AND PATTERN DISCRIMINATION

DISSERTATION

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the Degree Doctor of Philosophy in the Graduate
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FIELDS OF STUDY

Major Field: Physiological Psychology

Minor Field: Experimental Psychology

CONTENTS

TABLES

I. The problem

General statements (Marquis, 1932, Teuber, 1960, Morgan, 1965) regarding the role of the visual cortex in pattern vision stress the inability of animals with complete ablations of the striate cortex to learn pattern problems. This stress should not be interpreted as meaning that such lesions destroy all reactions to patterned stimuli.

Lashley's extensive work clearly demonstrated that rats which had sustained ablations of the visual cortex were unable to learn certain pattern problems (Lashley and Frank, 1934). Nonetheless, these animals were able to localize objects in space (Lashley 1934). After visual cortical gyrectomies, cats can still respond with optikinetic eye movements to moving striations (Smith, 1937). Cats can also discriminate a horizontal from a vertical bar, but after the addition of a second bar to the stimuli can not do so (Smith, 1938). After testing one of two occipitally lesioned monkeys on discrimination of various patterned configurations, Kluver (1941) concluded that "topographical aspects of the stimulus configuration" may be effective in determining the reactions of lesioned monkeys. Doty (1961) has reported some, although impaired, pattern discrimination learning in cats with degenerated lateral geniculate nuclei after visual decortication. Neodecorticated cats were found by Meyer (1963) to be unable to learn a stripe-check discrimination, but they could perform on a visual cliff as well as her normal group.

Hence, there seems ample evidence that animals deprived of their cortical visual projection areas may still respond differentially to some aspects of patterned stimulation. However, in 1941 Kluver cautioned that it served no purpose to say that such findings were indicative of rudimentary "pattern vision" since the problem is to find the properties of various configurations which are or are not effective in determining behavior. It was the aim of this study to further specify and delimit these properties.

II. Introduction

Interest in the role of cerebral cortex in vision was, according to a comprehensive review by Marquis (1932), awakened in the first half of the 19th century by the work of Flourens. Flourens reported that ablation of one cerebral hemisphere resulted in blindness of the eye opposite, and that after bilateral ablation blindness was complete in pigeons, rabbits or dogs. In the intervening century between these reports and Marquis' review, evidence accumulated that the blindness observed was not absolute; lid and pupillary reflexes were noted as spared. Many experimental studies tended to restrict the primary visual area of the cortex to the area anatomically delimited as the area striata, and in 1911, Minkowski presented precise experimental proof of this relationship. Even before Minkowski's demonstration of visual projection on the cortex, Munk had proposed a point-to-point projection and had attempted to explain the conflicting literature and sparing of reflexes with the concept of "psychic blindness." According to his approach, the cortex served a higher integrative function and injured animals could see but not "understand" the meaning of visual images. Because this general approach did not attract any considerable experimental support, and disputes continued over whether animals with cortical lesions could recover the ability to react to objects, interest turned to the particular specification of the abilities of animals which had suffered cortical ablations.

By 1932, the evidence on the visual abilities of rabbits with cerebral lesions was still confusing; some investigators had found them able to react to objects, others had not. Lashley, however, had begun his extensive experiments (1929 & 1931) with rats, and the conclusions were already clear. He found that bilateral destruction of the occipital cortex including all of the area striata did not impair the ability of a rat to learn a discrimination between light and dark. If the discrimination were learned preoperatively, it was lost but could be relearned. Lashley was unable to find any evidence of a postoperative ability of the rats to form pattern discriminations. Postoperatively Lashley's rats did seem to be able to distinguish position and, to some extent, the distance of their jumping platforms.

For dogs and cats Marquis did not find the experimental evidence uncontestable, but it did seem quite convincing that object vision was lost after bilateral striate ablation. There were suggestions that light-dark discriminations were spared and Marquis confirmed this sparing experimentally with dogs.

In the monkey the evidence was not clear cut but seemed to indicate that object vision was impossible with large cerebral lesions. Marquis knew of no studies of light discrimination with monkeys.

The clinical evidence in man indicated to Marquis that only pupillary reflexes were spared after destruction of the visual areas of the cerebrum. From these and other data which he cites, Marquis proposed that there was a phylogenetically progressive encephalization of visual function; more and more visual functions were taken over by the cerebral cortex until in man even light-dark discrimination was totally dependent upon the cortex.

Research since 1932 has served more to emphasize the similarities of cortical visual function in rats, cats and monkeys than to indicate a progressive encephalization. Additionally, it seems, as Smith (1937b, p. 360) stated "...that no distinct division of neural function is involved in the mediation of brightness discrimination and what has been discussed by Marquis as object vision."

This conclusion of Smith's was based upon an extensive series of experiments conducted primarily with cats (1936, 1937a, 1937b and 1938). Smith was able to demonstrate that under conditions of illumination and contrast comparable to those used in previous tests of object vision, cats with ablations of the cortical projection areas did not respond to objects, whereas under conditions of high contrast in illumination they were able to do so. Further,he showed that the ability of brain damaged cats to respond to light-dark discriminations could be disrupted by a high intensity surrounding illumination. Smith believed that Lashley's failure to find any evidence of pattern discrimination in striate ablated rats was also due to a lack of sufficient contrast within the stimuli and, in 1938, was able to demonstrate the ability of cats lacking the visual projection areas to discriminate a horizontal from a vertical bar, a condition of high spatial contrast. Earlier studies had also provided evidence of sparing of optikinetic reflexes to moving striations (Smith, 1937a).

Thus Smith believed that there was neither evidence for a progressive encephalization in the mammalian series nor any evidence for a separate encephalization of light and pattern vision; rather, the experimental findings seemed "...consistent in showing that extirpation of the striate areas, by reducing the efficiency of the entire optic system, brings about a limited disturbance in different visual functions rather than complete abolition of certain specific functions such as pattern vision" (1937b, p. 363).

In 1941, Kluver published a study of two monkeys that had sustained occipital lobe removal. One of the conclusions of this study is widely known; Kluver found that these monkeys did not respond to differences in brightness but only to differences in the density of luminous flux entering the eye. There was other information concerning the discrimination of form and position obtained from these monkeys; but because the results on form vision were not obtained after extensive postoperative training, Kluver considered them preliminary. However, he obtained definite differential responses to differing topographical arrangements of stimuli and clear evidence that the monkeys could respond to right or left positions of lights. Kluver treated the findings separately and made no comment upon their reconciliation. Kluver also found that high room illumination eliminated the monkey's differential responses.

In 1955, Denny-Brown and Chambers reported upon a series of limited cortical ablations in monkeys. Ablation of area 17 (the striate cortex) alone resulted in sparing of prehensile reactions to moving objects, in no recognition of still objects and in sparing of visual placing and optic righting. They too found that bright illumination inhibited the reactions. In this preparation the lateral geniculate nucleus was completely degenerated. Removal of the secondary projection areas (18 and 19) also left placing, righting and prehensile reactions intact but seemed to lead to impairment of spatial judgement and to confusion by moving objects.

A further theoretical argument has been advanced by

Doty (1961). He has proposed that the topographical arrangement of the retino-cortical projection is in itself of minor or no importance in the visual analysis of geometric patterns. To support this argument he has presented data from neonatal-and adult-operated cats which indicate that cortex other than the area striata (anatomically a point-to-point projection area) is necessary for visual pattern discrimination. Although Doty has not precisely specified the necessary areas for pattern vision, he has indicated that areas lateral to the primary cortical projections may be essential for pattern discrimination.

Meyer (1963) has reported that cats with ablations of most of the neocortex were unable to learn a pattern problem involving a local brightness controlled discrimination between striped and checked patterns. These cats performed successfully in a light avoidance task and did not differ from the normal group in responses to a visual cliff. Although there are many cues to depth in a natural situation the arrangement in this case seemed to have allowed the response to be based only upon some type of perception of pattern.

Depth discriminations and even visual placing reactions might reasonably be assumed to be dependent upon much the same mechanisms as pattern discrimination (see Gibson and Walk, 1960, on the importance of textural cues in the visual cliff). Hence a reasonable approach to characterizing the contributions of the visual cortex to the discrimination of patterns seemed to lie in a comparison of depth and pattern problems. It also seemed reasonable to investigate visual placing reactions since in brain damaged cats Smith had found them absent (1936) while in Doty's animals they were present (1961). In Meyer's neodecorticate cats they were absent under normal conditions but recoverable under the influence of dl-amphetamine (Meyer, Horel and Meyer, 1963).

III. Subjects and surgery

The *Ss* were 20 adult cats. One, VC 23, had been trained on the stripe-check discrimination prior to surgery.

In 10 cats, cortex from the lateral and suprasylvian gyri was aseptically removed by subpial aspiration under sodium pentobarbital anesthesia. The lesions were intended to encompass the striate cortex and all secondary projection areas defined by Buser and Borenstein (1959) except those on the ectosylvian gyrus. The cats were allowed at least six weeks recovery before testing.

IV. Apparatus and procedures

The ten operated cats were tested simultaneously with the normal control Ss on a variety of tasks. Essentially these tasks involved a pattern problem, responses to a visual cliff, visual placing and performance upon a horizontal adaptation of a visual cliff to a conventional discrimination task in which the multiple cues associated with visual cliff performance could be controlled and reduced to their pattern components.

Experiment I

The normal (NC) and operated (VC) cats were allowed 500 trials to discriminate striped from checked doors (cf. Meyer, 1963) in a Yerkes-Watson-Munn box similar to that described by Aarons and Reisen (1959). Hinged stimulus doors, which concealed 2-gm. pieces of fish, were lighted from above and positioned according to a Gellerman-type series. After preliminary training with white doors, the cats were given 10 correction trials per day for 5 days per week until 500 trials or a criterion of 18-correct-out-of-20 was reached.

Experiment II

A glass-covered 24 x 48 x 30 in. black-and-white-checked plywood box with a translucent plexiglass checked floor served as a visual cliff. The checks, like the checks on one of the doors in Exp. I, were 3 x 3 in. A trapezoidal starting platform 6-in. high, and set atop the glass, divided the box. On one side of the platform, a plexiglass floor was set immediately below the glass (shallow side); while on the other, it rested 30-inches underneath the glass (deep side). The cats were placed on the platform and allowed to descend to the glass on whichever side they chose once a day for 18 days. Three conditions of luminance (shallow and deep respectively 0.87 and 1.78 log. ft. lamberts; both 1.78 log. ft. lamberts; and shallow and deep respectively 1.78 and 0.87 log. ft. lamberts) and right and left positions of the shallow side were varied according to a latin square.

Experiment III

The cats, supported as to permit them only to place by way of visual cues, were presented to tooth-edged boards within a grey booth 15 times a day for 10 days. Randomly ordered presentations of three boards (black, grey or white) at three heights (24, 36 or 48 inches) or no boards controlled stereotyped responding.

Experiment IV

Transilluminated, 30-in. deep black-and-white checked boxes replaced the 9 x 12 in. hinged stimulus doors in the discrimination box for this experiment. Dispensers directly over the stimuli dropped the reinforcements (2-gm. pieces of fish) in front of the stimuli. After 10 days of preliminary training with white stimuli, the cats were reinforced for a response to either a checked pattern directly behind (shallow) the clear plexiglass front of the stimulus boxes or to one placed at a distance of 30-in. (deep) from the front.

During this training to a 45-correct-out-of-50 criterion, the total amount of light from each stimulus remained equal. The luminance on the shallow and deep sides respectively were 1.4 and 2.5 log ft. lamberts from the white portions. Tests were then made with the luminance of both stimuli at 1.4 log. ft. lamberts. If a cat did not achieve 9/10 correct on the test within 30 trials, it was returned to the original problem and retrained to a 9/10 criterion, then retested. All subsequent brightness or local brightness tests were conducted in the same manner.

A succession of brightness tests were conducted after completion (criterion, 9/10 on any one day) of each previous test. To minimize, if not eliminate, the illumination gradient along the sides of the deep box, the stimuli were front- as well as trans-illuminated. Rheostat settings were reversed (deep, 2.5 log. ft. lambert; shallow, -0.1 log. ft. lamberts) and then a test was conducted with luminance matched, the front lights on, but the black and white portions of the stimuli interchanged.

If discrimination was not disrupted by brightness or local brightness tests, a second problem was presented. The shallow stimulus (3 x 3 in. checks) remained the same but a two-dimensional projection of the deep stimulus, presented immediately behind the clear front panels, was substituted for the deep stimulus.

If a cat was able to discriminate these stimuli and discrimination was not disrupted by local brightness tests, a panel containing 1½-inch checks was substituted for the simulated deep stimulus.

If the cat discriminated these stimuli through local brightness tests, four orientations of 1½ inch stripes were substituted for the small checks and, finally, four orientations of 3-inch wide stripes were substituted for the smaller stripes (a problem similar to that of Experiment I).

Histology

After the behavioral testing was complete, the operated animals were perfused with saline and 10% formalin and their brains were then removed and fixed in 10% formalin. The lesions were diagrammed and the brains were photographed under an ultraviolet light source which accentuated the contrast between the damaged and undamaged areas. The brains were embedded in celloidin and sectioned at 30 microns. Every twentieth coronal section through the lesion and every fifth section through the lateral geniculate nuclei was stained with cresylecht violet.

V. Results

Experiment I

Table 1 gives the positive stimulus and the number of trials to three criterion measures for each cat. All of the operated animals were severely impaired in discriminating stripes from checks. However, three of the VC cats showed some evidence of learning, and of these the animal (VC 23) which had had preoperative training performed best.

Experiment II

Eight of the 9 normal animals descended consistently on the shallow side of the visual cliff. Cat NC 2 position responded. The operated cats, however, made significantly ($U = 14$, $p < .02$) more responses to the deep side. Luminance variations did not affect the choices indicated in Table 2.

Experiment III

All 15 cats visually placed. The normal cats were somewhat inconsistent and the difference between the groups was not significant ($t = 1.44$, $df = 13$). The percentages of placing reactions observed during 150 tests per animal are presented in Table 3.

Experiment IV

In the first day's session of the deep-shallow discrimination task 7 of 8 normal cats chose the deep side more than half of the 10 trials. Only VC 15 and VC 17 showed this preference in the decorticate group.

TABLE 1: Experiment I: Trials to 3 criterion measures.

		Positive stimulus	Criterion 1[a]	Criterion 2[b]	Criterion 3[c]
Normal cats	NC1	checks	31	80	80
	NC2	stripes	28	-[d]	-
	NC3	checks	81	370	370
	NC4	checks	90	90	190
	NC5	stripes	242	440	470
	NC6	stripes	377	380	380
	NC7	stripes	167	310	420
	NC8	checks	362	430	-
	NC9	checks	94	210	310
Visually decorticated cats	VC15	checks	344	-	-
	VC16	stripes	-	-	-
	VC17	stripes	-	-	-
	VC18	checks	-	-	-
	VC19	checks	-	-	-
	VC20	checks	-	-	-
	VC21	checks	423	-	-
	VC22	stripes	-	-	-
	VC23	checks	73	430	430

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[a] Criterion 1: 9-out-of-any-10 correct. Touching of incorrect door recorded as an error.

[b] Criterion 2: 9-correct-in-any-10-trial-session. Touching of incorrect door recorded as an error.

[c] Criterion 3: 9-correct-of-any-10-trial-session. Incorrect alley entry recorded as an error.

[d] Did not meet criterion in 500 trials.

TABLE 2. Percent responses to the shallow side of the visual cliff for each cat.

Normal cats								
NC1	NC2	NC4	NC5	NC6	NC7	NC8	NC9	NC10
100	61	100	100	100	100	100	100	100
Visually decorticated cats								
VC15	VC16	VC17	VC19	VC20	VC21	VC22	VC23	VC24
100	94	61	39	33	78	61	39	78

TABLE 3. Percentage of occasions upon which visual placing was observed in 150 tests.

Normal cats

NC1	NC2	NC4	NC5	NC6	NC7	NC8	NC9
82	99	87	84	96	71	87	34

Visually decorticated cats

VC15	VC16	VC19	VC20	VC21	VC22	VC23
38	75	75	25	88	94	41

As Table 4 indicates, normal cats learned the deep-shallow discrimination quickly. The visually decorticated cats also learned the discrimination but required many more trials.

Two cats (VC 16 and VC 22) did not meet criterion within 500 trials, but after special training did discriminate these stimuli. In this training VC 16 first learned a black-white discrimination; then, after training with combined depth and brightness cues, VC 16 was still able to discriminate when the brightness cues were removed. Cat VC 22 responded differentially to the depth cues but always first entered the left alley. Thus, if reinforcement was withheld for 5-sec., and the left stimulus was positive, the cat waited in that alley. If the left stimulus was negative, the cat went to the other stimulus in less than 5-sec. Indications of differential responding hence were obtained by timing the cat's left alley response in further testing.

Cat VC 23 did not meet a 45-correct-out-of-50 criterion in 1000 trials and was not further tested. Cat VC 17 died before testing was complete.

Changes in lighting affected only the performance of VC 20. However, after extensive training with gradual changes in lighting, its performance became independent of any changes. Reversal of the black and white portions of the stimuli had no effect with any cat.

TABLE 4. Experiment IV: Deep-shallow discrimination. Positive stimulus and trials to two criterion measures.

		Positive stimulus	Criterion 3[a]	Criterion 4[b]
Normal cats	NC1	shallow	40	50
	NC2	shallow	30	210
	NC4	deep	0	150
	NC5	deep	0	230
	NC6	deep	40	30
	NC7	shallow	120	150
	NC8	shallow	20	20
	NC9	deep	10	130
Visually decorticated cats	VC15	shallow	80	170
	VC16	shallow	-[c]	-[c]
	VC17	deep	270	Died
	VC19	deep	390	460
	VC20	shallow	440	440
	VC21	deep	140	320
	VC22	shallow	-[c]	-[c]
	VC23	shallow	490	-[d]

[a] Criterion 3: 9-of-any-10-trial-session correct. Incorrect alley entry recorded as an error.

[b] Criterion 4: 45-of-50-trials in five sessions correct. Incorrect alley entry recorded as an error.

[c] Met criterion after special training.

[d] Did not meet criterion in 1000 trials.

When a two-dimensional projection of the deep stimulus was substituted for the deep stimulus proper, all normal and 5 of the 6 remaining decorticates met criterion (9-correct-out-of-10) within 60 trials. Cat VC 22 met criterion at 400 trials but its performance was unstable during testing with reversals of the black-white portions of the stimuli. No determination of the influences of these cues could be made and the cat was not further tested.

When the 1¼-in. check pattern was substituted for the two-dimensional projection of the deep stimulus, all normal and 3 decorticated (VC 15, VC 19, VC 21) Ss again transferred quickly. Cat VC 16 met criterion after 240 trials, but its performance was unstable and no determination of the influence of brightness cues could be made. Cat VC 20 could not discriminate these stimuli within 310 trials.

Transfer to a discrimination in which 1¼-in. stripes were substituted for the 1¼-in. checks was more difficult (one normal cat required 190 trials). Three operated cats were tested; VC 21 did not meet criterion in 510 trials. Although VC 19 met criterion its performance was unstable and the influence of brightness cues could not be determined. The remaining operated cat (VC 15) was able to discriminate these stimuli and the 3-in. stripes from 3-in. checks.

Although unstable performance sometimes accompanied the brightness variation in this experiment, there was no clear evidence that any cat was responding to local brightness cues. Overhead lighting rather than transillumination had no effect.

A summary of the results from operated cats in this phase is given in Table 5. All normal cats discriminated these stimuli.

Histology

The extent of the striate cortical lesions was judged by examination of retrograde degeneration in the dorsal lateral geniculate nuclei. Table 6 presents the percentages of sparing of the cells within these nuclei except in the instance of VC 24, which died unexpectedly.

Rank-order correlations of visual cliff, visual placing and Experiment IV performance with the extent of lateral geniculate damage were obtained. The correlation between visual placing and lesion extent was not significant ($r_s = +.66$, $p > .05$). Significant correlations were obtained between visual-cliff performance and lesion extent ($r_s = +.87$, $p < .01$) and ultimate performance in Experiment IV and lesion extent ($r_s = +.75$, $p < .05$).

TABLE 5. Experiment IV: Summary performance for each lesioned cat. "D" indicates successful completion of the problem and local brightness tests. Normal cats were successful on all problems.

	Deep vs. shallow	Large checks vs. simulated deep	Small vs. large checks	Small stripes vs. large checks	Stripes vs. checks
VC15	D	D	D	D	D
VC16	D	D			
VC19	D	D	D		
VC20	D	D			
VC21	D	D	D		
VC22	D				
VC23					

TABLE 6. Percentages of the dorsal lateral geniculate nuclei undegenerated in lesioned cats.

Lesioned cat	% spared, left	Left nucleus: location of sparing	% spared, right	Right nucleus: location of sparing
VC20	0		4	anterior ventral
VC23	8	anterior ventral, posterior dorso-lateral	4	posterior dorso-lateral
VC19	11	anterior, anterior ventral, posterior	14	anterior, anterior-ventral, posterior
VC16	16	anterior, anterior ventro-lateral, posterior	10	anterior
VC22	12	anterior ventral	20	anterior & posterior
VC21	35	anterior & anterior lateral	22	anterior
VC17	60	anterior, anterior ventral, & ventro-lateral	36	anterior ventral, & ventro-lateral
VC18	57	anterior dorso-lateral, lateral & posterior	65	anterior lateral, & posterior
VC15	18	posterior ventral	80	anterior, ventral & posterior

VI. Discussion

In review, these lesioned cats were able to perform certain behaviors which appear to be dependent upon a modicum of form perception. They were least impaired in visual placing, a performance which was not expected to be spared except in preparations which were subtotal (Bard and Orias, 1933). At least some portions of the LGN's were intact in all the present operated group; however, VC 20 with the most complete ablation and only 4% of the right LGN remaining placed on 25% of the tests.

Visual cliff performances were more impaired than those observed by P.M. Meyer (1963), despite the fact that her cats had sustained ablations of more cortex. However, the test methods differed; in Meyer's cliff, deep choices were punished by a fall, whereas in this experiment the consequences of a choice were identical. The difference in results may be a function of these situation differences since cats in the present study could distinguish deep from shallow stimuli in a discrimination situation.

The cats were severely impaired in the check versus stripe problem. Two operated cats with considerable cortical sparing met only a weak criterion. VC 23, which learned, had little cortical sparing but was unique in that it had had extensive preoperative training on the problem.

However, cats that failed this problem did discriminate between the deep and shallow alleys and transferred that discrimination (with the exception of VC 23 and VC 22) to the check versus two-dimensional projection of the deep stimulus problem.

The question, then, is whether the configuration of the cues in a two-dimensional projection of a cliff or the deep and shallow alleys needs to be appealed to as a factor in sparing of discrimination. If so, then the lesioned animals should not have transferred to the $1\frac{1}{4}$-in. checked pattern. However, 3 of 5 animals did transfer. Two of these subsequently failed to transfer to the $1\frac{1}{4}$-in. stripe problem and this problem was successfully completed by only the cat which had 80% of the LGN spared unilaterally.

The most parsimonious assumption is that these results are all consistent with the view that animals with striate lesions still are capable of visual discriminations of stimuli which contain different contour lengths. This is a common property of all the discrimination problems in the study.

Contour length varied even in problems which most lesioned cats failed. However, the ratios of contour difference were not the same in all problems. In the stripe-check problem this contrast in total contour length was highly variable because of the use of multiple stimuli for local brightness control and the mean ratio of differences was 1:2. The contrast was also variable and very small (mean 1:1.3) in the $1\frac{1}{4}$-in. stripe-3-in. check problem which only one lesioned cat discriminated. The other problems had constant and larger ratios; the ratio in the $1\frac{1}{4}$-in.-3-in. check problem was 1:2.3 and in the two-dimensional projection situation was 1:4.3.

Hence the correlation of lesion extent with ultimate performance in Experiment IV appears to indicate that ability to discriminate contour differences is decreased by more and more severe geniculo-striate ablation in these cats.

Similarly, Weiskrantz (1963) found that a young monkey with striate cortex ablation could discriminate stimuli which differed substantially in total contour length. Interestingly, one of the occipitally lesioned monkeys tested by Kluver (1941) was able to discriminate a square from a configuration of 76 circles having the same total area, but not a square from a cross of equal area.

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