

THE UNIVERSITY OF CALGARY

THE EFFECTS OF LESIONS TO CORTICAL AND
SUBCORTICAL VISUAL AREAS ON A CONDITIONED
EMOTIONAL RESPONSE TO A LIGHT STIMULUS

by

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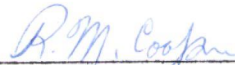
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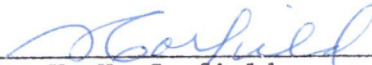
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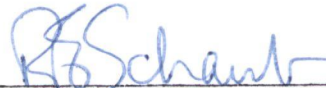
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "The Effects of Lesions to Cortical and Subcortical Visual Areas on a Conditioned Emotional Response to a Light Stimulus" submitted by Jacqueline Ann Battistella in partial fulfillment of the requirements for the degree of Master of Science.



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ABSTRACT

The study assessed the notion that the visuosensory aspects of habits that are guided by diffuse light are mediated by the pretectal area while those that are guided by spatial light arrays are mediated by visual cortex. Rats were trained to perform a conditioned emotional response (CER) to a light stimulus under two visual conditions. In one condition unrestricted vision was allowed, in the other condition rats wore light-diffusing masks over their eyes. In various experiments the rats were given either visual cortex or pretectal brain lesions and postoperative retention of the CER was examined.

The results only partially supported the hypothesis under test. Occluded animals did retain the CER better after cortical lesions than did unoccluded animals, as the notion predicts. After pretectal lesions, however, and at variance with the hypothesis, occluded animals were no more impaired than the unoccluded animals.

The results lead to reconsideration of previous findings that were taken as support for the idea that the pretectal area is particularly important for mediating the visuosensory aspects of diffuse light habits. An alternative interpretation of the earlier findings is proposed. This includes the idea that occluded animals, if they are to perform certain visual discrimination tasks, must make different responses than unoccluded animals, and it is a neural mechanism underlying these responses, rather than the animal's vision per se that is disrupted by pretectal lesions. This new interpretation was suggested not only by the failure to confirm predictions from past work but also by the observation of a nonvisual impairment in the CER situation.

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CHAPTER I

INTRODUCTION

Statement of the Problem

A number of researchers have suggested that the cortical and subcortical parts of the visual system carry out different functions. The present study is an assessment of one such view which suggests these functions are determined by the nature of the visual cue. According to this view, visual cortex predominates when the critical cue consists of the spatial attributes of the visual discriminanda, and the subcortical pretectal region predominates when the critical cue is light intensity.

Historical Overview

Despite an extensive literature on the vertebrate visual system, the exact contributions of its cortical and subcortical components to visually-guided behaviour remain to be elucidated. One approach to the problem aims at ascribing specific roles to either cortex or subcortex. Thus the classical view of visual system functioning suggests that visual cortex provides the organism with visual percepts or visual objects while subcortical visual areas carry out a supportive role mediating such responses as eye movements and the pupillary reflex.

Since the pioneering work of Lashley (1920), Marquis (1934) and Klüver (1942), however, it has been apparent that the function of subcortex may be far less restricted than the classical position suggests. Visually decorticate rats, cats and monkeys are quite capable of some visual discriminations, and, do particularly well when

light intensity differences predominate among the visual stimuli.

The status of humans with visual cortical damage is less clear. In line with the classical view, it has frequently been reported that visual cortical lesions induce complete blindness. Recent work, however, undermines this conclusion, as it now seems that residual vision remains in man following such damage (Weiskrantz, Warrington, Sanders & Marshall, 1974). Consequently, even in man, subcortical visual structures may contribute more to vision than the classical position allows.

The animal work in particular has led to the gradual adoption of the view that all visuosensation is not critically dependent on the cortical visual areas. Hence, diverse functional models have evolved as attempts to specify the contributions of cortex and subcortex to visually-guided behaviour. The present study is specifically concerned with one notion which suggests that these contributions are determined by the nature of the visual cue.

Anatomy of Visual Cortex

In Figure 1 the major afferent pathways of the visual system are schematized. In mammals many retinal ganglion fibres terminate subcortically in the dorsal lateral geniculate nucleus (LGN_d), (Polyak, 1957). In turn, cells of this nucleus send axons largely to Brodmann's area 17 ("striate" or "primary" visual cortex). Fibres from area 17 project to areas 18 and 19 (visual "association" cortex).

Until recently, the only known route from the eye to areas 18 and 19 was via area 17. However, an indirect retinal-pulvinar route to

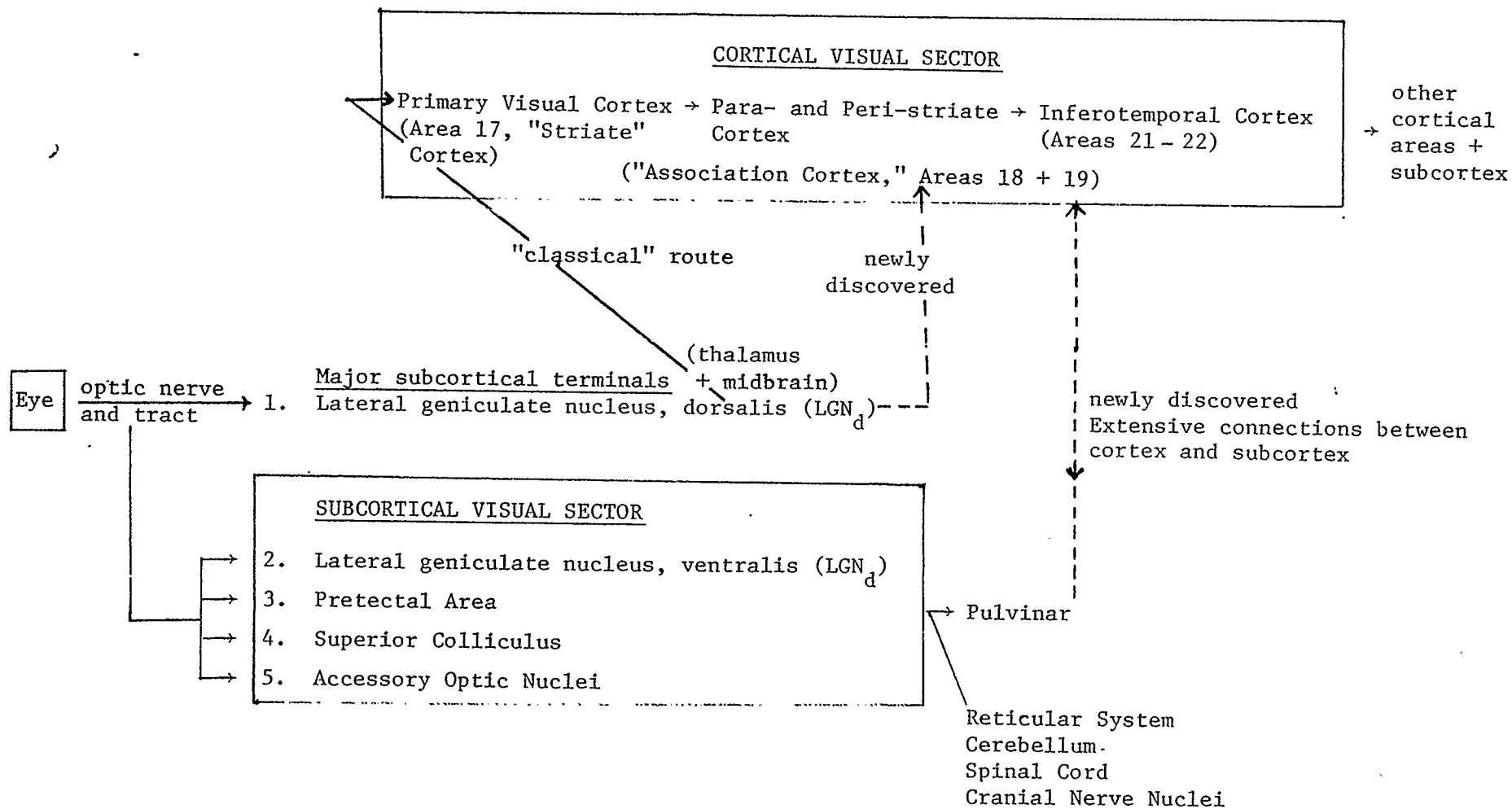


Figure 1. Major Afferent Pathways of the Visual System

areas 18 and 19 has now been verified in monkey (Benevento & Rezak, 1976), opossum (Benevento & Ebner, 1970) and cat (Graybiel, 1972). Given the intimate anatomical associations between the eye and areas 17, 18 and 19, it seems appropriate to refer to the latter areas collectively as "visual cortex." While this definition of visual cortex is adhered to in this thesis, it should be noted that some researchers still use the terms visual cortex and area 17 synonymously.

Klüver's Position

Based on an extensive investigation of the visuosensory capacities of monkeys with large lesions to areas 17, 18 and 19, Klüver (1942) concluded that such animals lacked even a rudimentary visual world, and were reduced to responding to differences in the amount of light energy, or luminous flux, hitting the retinae. Thus, while intact and visually decorticate monkeys could both be trained to respond to the brighter of two lighted panels of the same size, Klüver showed that in such a task the intact animal used brightness as the behaviourally effective cue, while the decorticate animal used light intensity. Specifically, intact animals could maintain their performance even when the brighter stimulus was moved a certain distance from the animal, such that the amount of light energy striking the eyes from both light panels was equated, while decorticate animals could not.

Needless to say, and consistent with his position, Klüver also found that visually-decorticate monkeys could not discriminate on the basis of movement, form, size and distance, that is, on any visual dimension with a spatial aspect to it. Klüver supposed the cortical

visual areas were essential for imposing a spatial structure on a more primitive sensation of light energy, thereby providing the organism with visual objects.

Klüver also found that the absolute light-intensity thresholds of his decorticate animals were comparable to those of intact animals. This indicates that the intensive aspect of visuosensation is not impaired by visual decortication, and raises the possibility that this visual dimension is mediated subcortically in the intact animal, a point of central concern in the present study.

Research Supporting Klüver's Position

Stripes discrimination habit. Horel, Bettinger, Royce and Meyer (1966) trained intact rats to discriminate between cards that had stripes placed at different angles. The use of local intensity cues was prevented by having two positive and two negative cue panels, with one of each type beginning with a black corner, and the other with a white corner. Thus these animals had to discriminate between two panels of stripes that always ran in opposite directions, yet varied with regards to local intensity cues. Following large visual cortical lesions, these animals lost the habit and could not reacquire it. Naive visually decorticate rats also failed to acquire this task. Horel et al.'s findings were confirmed by Bland and Cooper (1969) who also showed that even when the cortical visual areas are removed neonatally, the acquisition of a stripes discrimination is prevented.

The occluded sparing phenomenon. Several studies undertaken by Cooper and his associates report findings that again suggest that

spatial vision is critically dependent on the cortical visual areas, while the intensive aspect of vision is not. Bauer and Cooper (1964), for example, used shock motivation and trained rats wearing light-diffusing occluders and rats wearing visually unrestrictive eye-pieces to approach a lighted panel and avoid a darkened one. The occluders were used in an attempt to minimize the visuospatial aspects of the discriminanda, thereby forcing the discrimination to be made on the differences in the amount of luminous flux (light intensity) hitting the retinae. After reaching criterion the occluded and unoccluded animals received large visual cortical lesions. Postoperative testing revealed that the occluded rats had good sparing of the habit, while the unoccluded rats did not. In a similar study, Cooper, Blochert, Gillespie and Miller (1972) used food rather than shock avoidance as the incentive for learning, and provided further confirmation of the occluded sparing phenomenon.

Such findings are accountable for by supposing that cortical visual lesions differentially affect the unoccluded and occluded light-dark habits because of the nature of the visual cue utilized during task acquisition. That is, animals with unrestricted vision are more impaired transoperatively, as the lesion forces a change from spatial to intensity cues. Occluders by forcing the use of light-intensity cues protect the habit, in the sense that no change of cue is induced by the cortical lesion. Consequently, no shift from cortical to subcortical mediation of the habit is required.

Electrophysiological support. Visual cortical cells in mammalian species as diverse as the mouse and the monkey are reported not to

respond to general illumination changes (e.g., Dräger, 1975; Hubel & Wiesel, 1959). These cells fire best to slits of light, dark bars and edges at particular orientations. In addition, many researchers (e.g., Hubel, 1963; Rodieck, 1973) have noted that there is a progressive selection against light intensity per se at each step of the afferent visual pathway. Thus, if the receptive field of a specific cell is flooded with diffuse light, at the retinal ganglion level there is a weak response, at the lateral geniculate nucleus a weaker one, and, at the cortical level no response at all, or a very minimal one.

Such a selection against diffuse light in favour of spatial distributions of it, suggests that visual cortical cells are predominantly concerned with a spatial analysis of the visual environment. Nevertheless, the evidence is not conclusive. The minimal firing that occurs in a few cortical cells to diffuse light may be sufficient to convey information about so simple a dimension of vision as intensity.

A Brief Overview of Alternate Views as to the Contributions of Cortex and Subcortex to Visually-Guided Behaviour

Marquis and Hilgard (1936) trained intact dogs to perform a conditioned eyeblink to a light CS then subjected the animals to extensive visual cortical lesions. Postoperatively, when the light CS was presented good retention of the habit was evident. Such findings are consonant with the notion (e.g., DiCara, Braun & Pappas, 1970; Steele Russell, 1971) that classically conditioned responses are mediated subcortically. Wing (1947), however, found that dogs trained to lift the left hind leg to obtain food reinforcement retained the CR

to a light onset or to a change in light intensity, following removal of the cortical visual areas. These habits were not classically conditioned, yet they survived visual decortication. Hence, notions which suppose subcortex can only mediate classically conditioned habits are not supported by this work.

Many researchers (e.g., Horel et al., 1966; Lashley, 1935; LeVere & Morlock, 1973) have assessed the contribution of the cortical visual areas to visually-guided behaviour by training animals, usually rats, to approach a lighted panel and avoid a darkened one. When this habit is acquired by intact animals with unrestricted vision, large visual cortical lesions disrupt performance yet postoperative training reinstates criterion performance. Interpretations of the deficit and the subsequent recovery of the habit have often been couched in memory terms (e.g., Lashley, 1935; Meyer, 1972).

The postulated memory function of visual cortex encounters certain difficulties. Lashley, for example, proposed that the memory trace for the light-dark habit is located in visual cortex, while its visuosensory aspects are mediated subcortically. This notion must suppose that the memory trace for the occluded version of the light-dark task is also located in visual cortex. Hence, it does not satisfactorily explain the fact that occluders protect the light-dark habit against the effects of visual decortication.

While the alternative sensory loss hypothesis of Bauer and Cooper (1964) provides a more parsimonious account as to the role of visual cortex in the light-dark habit, it nonetheless, has certain difficulties.

Specifically, its explanation of the fact that visually decorticate and naive intact rats can have comparable acquisition functions is not entirely satisfactory. Presently, it must suppose that the seemingly essential cortical participation in the light-dark habit of the intact animal with unrestricted vision is determined by the spatial aspects of the discriminanda. Hence, if the visually decorticate animal has access only to the intensive dimension, it is, in fact, using a visually degraded cue. Therefore, such an animal should not acquire the habit with a facility that is comparable to that of the intact animal. Despite such considerations, this notion has a clarity that is often wanting in accounts as to the roles of cortex and subcortex in visually-guided behaviour.

Anatomy of the Pretectal Region of the Subcortical Visual System

The subcortical sector of the visual system consists of four major structures that are terminals for retinal fibres (see Figure 1). Since the present study is particularly concerned with the pretectal region the anatomy of this region is emphasized.

The pretectal region consists of a group of nuclei situated in the transitory zone between the thalamus and the superior colliculus. While evident in all mammals, its boundaries are ill-defined, and, between species there are wide variations in the size, shape and location of its nuclei (Carpenter & Pierson, 1973; Scalia, 1972).

In the rat, mouse, rabbit and tree shrew the predominant retino-pre-tectal terminals are the nucleus of the optic tract and the olivary nucleus, while the posterior pretectal nucleus receives a sparser

projection (Hayhow, Sefton & Webb, 1962; Scalia, 1972). In the higher primates a diminution of retino-pretectal fibres is noted (e.g., Giolli & Tigges, 1970) but the nucleus of the optic tract, the olivary nucleus and the sublentiform nucleus remain generally recognized as retinal terminal sites (Carpenter & Piersen, 1973).

Research Indicating That the Intensive Dimension of Vision is Mediated by the Pretectal Region

Behavioural support. Thompson and Rich (1963) found that lesions to the pretectal region disrupted postoperative performance of a dark grey vs white card habit more severely than a stripes habit. Further substantiation of this finding was provided by Peters and Cooper (1969) who found that pretectal lesions disrupted a black vs white card discrimination more than a stripes discrimination. Such findings encourage the view that the pretectal region is involved in mediating the intensive aspects of vision since the tasks which emphasized intensity differences were most impaired by lesions to this area.

Blochert, Ferrier and Cooper (1976) carried out a more direct test of the pretectal area's role in mediating intensity discriminations. Translucent occluded rats and rats with visually unrestrictive head pieces were trained to perform a two-choice, light-dark task, while another group of rats acquired a stripes discrimination. The occluded and stripes tasks were of comparable difficulty, in that the errors to achieve criterion were similar. After acquiring the habits, the experimental animals received pretectal lesions. Postoperative testing revealed that the pretectal lesions disrupted the performance of the

occluded, diffuse light habit more than that of the stripes or unoccluded light-dark habit. Since these effects were the opposite to those of cortical visual lesions, Blochert et al. inferred that the pretectal region subserves a critical visuosensory role in light intensity discriminations.

Electrophysiological support. Siminoff, Schwassmann and Kruger (1967) and Straschill and Hoffman (1969) found some cells in the pretectal region of the rat and cat seemingly designed for handling variations in light intensity. These cells responded tonically to diffuse lighting or dimming of their receptive fields. Moreover, some of these cells had large receptive fields that covered as much as 120° of the visual field. Such findings do indicate that the pretectal region could be involved in mediating the intensive dimension of vision.

Research That Opposes the Cortical-Spatial, Subcortical-Intensity Dichotomy

Several studies have challenged the notion that all spatial vision is critically dependent on visual cortex. However, most of these claims that attribute a modicum of spatial vision to the visually decorticate animal are not convincing. First, as Ferrier and Cooper (1976) noted, many apparent spatial discriminations could have been solved on flux information alone. Second, before a role in mediating spatial vision can be assigned to subcortex, all of areas 17, 18, 19 (areas 17, 18, 18a in the rat) must be ablated. Yet, typically, complete ablation of area 17 is reported, along with varying degrees of damage to areas 18 and 19. Hence, even if spatial vision were convincingly demonstrated in such animals, it could be mediated by remnants of areas 18 and 19 that are

innervated by the indirect retinal pathway, rather than by subcortex.

Ferrier and Cooper (1976) circumvented the problems alluded to above. Rats with complete ablations of areas 17, 18 and 18a were trained to jump 15 inches to an illuminated 2.5-in x 3-in panel to escape/avoid shock. Independent manipulation of spatial and intensity cues showed that the visually decorticate rats jumped to the position of the lighted panel and hence showed that these animals had at least some rudimentary spatial vision.

By clearly demonstrating that visually decorticate rats have some spatial vision, Ferrier and Cooper compromised the position which supposes that spatial vision is solely mediated by the cortical visual areas. Moreover, in certain situations (e.g., Cooper et al., 1972), transoperative performance deficits do occur in occluded animals following large visual cortical lesions. Thus, the claim that the intensive aspect of vision is solely the domain of subcortex is also not always convincingly supported.

Such findings indicate that what might be called the "cue hypothesis," the hypothesis that visual space is a function of cortex and intensity a function of subcortex, needs further testing.

Purpose of the Present Study

Studies that have manipulated the visual cues available to rats (Bauer & Cooper, 1964; Blochert et al., 1976; Cooper et al., 1972) have shown that cortical visual lesions and pretectal lesions differentially affect the occluded and unoccluded versions of the two-choice, light-dark habit. The cue hypothesis suggests these differential lesion

effects are accountable for in visuosensory terms; if this is the case, the effects should be evident in other visual tasks that make different learning demands on the animal.

The present study used a different task, the conditioned emotional response (CER) situation, and essentially provided a further test of the cue hypothesis that supposes the nature of the effective visual cue determines whether the cortical or subcortical sector of the visual system predominates in visuosensory processing.

CHAPTER II

EXPERIMENT 1

Gillespie and Cooper (1973) trained intact and visually decorticate rats to perform a conditioned emotional response (CER) to a light conditioned stimulus (CS). Providing the position of the light CS remained constant for both CER training and extinction, the extinction functions of these two groups were comparable. However, when the position of the light CS was shifted laterally 5 cm for the extinction phase of the experiment, the intact animals extinguished their CER much faster than the lesioned animals. This finding suggests that the intact animals were more responsive than the visually decorticate animals to spatial cues.

If intact rats use spatial cues in the CER situation, the cue hypothesis predicts that a preoperatively acquired CER to a light CS should be impaired by a visual cortical lesion. The present experiment assessed this possibility.

MethodSubjects

Six naive, black-hooded rats, approximately 100 days old at the start of the experiment, were gradually reduced to 75% of their initial body weight and maintained at this level throughout testing. However, during rest and recovery periods weights were increased to 85%.

Apparatus

The apparatus consisted of three Grason-Stadler Skinner boxes

enclosed in sound-attenuating cases, with fans providing a background noise level of about 60 db. The 1-min CS was provided by a 117-V, 7-W lamp, mounted 2.5 cm to the left of the lever, and 8 cm above the grid floor, the lamp emitted 8 ftc (86 lux) at source. Behavioural Apparatus shock generators were set at source to provide the unconditioned stimulus (US), a .5-sec, 150-mW grid shock that was delivered at the end of the 1-min CS interval. Programming and recording equipment was located in an adjacent room.

Surgery

After the animals had been conditioned to the light CS, they were anesthetized with sodium pentobarbital (60 mg/kg), secured in a Krieg Stereotaxic instrument, then, using the aspiration technique, an attempt was made to remove all neocortex located between the bregmoid and lamboid sutures, and laterally to the rhinal fissure. This neocortical area encompasses all of visual cortex.

Procedure

Pretraining. In the first session, the animals were magazine trained with 45-mg Noyes food pellets delivered automatically on a variable interval (VI) 1-min schedule. This session terminated after an animal had received 60 pellets. During the next four sessions, the animals earned 100 pellets on a continuous reinforcement schedule (CRF). The next four training sessions were of 60-min duration, and a VI 30-sec schedule, used throughout the rest of the experiment, was operative.

CER training. For two days, the light stimulus (CS) that was to

be used in conditioning was superimposed on barpressing, with animals receiving two 1-min presentations of the CS alone each day. On the next five days, the two daily CS presentations coterminated with the delivery of the .5-sec, 150-mW grid shock (US). Conditioning to the CS was assessed by the ratio of presses made during the 1-min CS, to presses made in the 1-min period immediately prior to the CS. Using this method, a ratio of 1.00 indicates the CS does not affect the ongoing barpress response, while a ratio of .00 indicates complete suppression of barpressing and conditioning to the CS. For each animal a daily ratio was obtained, by adding the responses made during the two CS presentations, and dividing by the responses made in both pre-CS periods.

The six animals were then divided into two groups that were matched on the basis of their rate of acquisition of the CER. One group received large visual cortical lesions, while the other served as an intact control group. After a 14-day recovery period, the animals were returned to the Skinner boxes, and, following four sessions of VI training, tested for retention of the CER. This test was one of extinction, as the CS presentations were not followed by shock during the five test sessions.

Histology

After completion of the CER extinction test, the lesioned animals were heavily sedated with ether, then perfused through the heart with physiological saline followed by 10% formalin and the brains removed.

Results

Anatomical

Inspection of the brains of the three lesioned animals revealed that the neocortical lesions were as intended with no apparent damage to the underlying hippocampus.

Behavioural

In Figure 2 the mean suppression ratios for the two groups are presented. As Figure 2 illustrates, the performance of the lesioned group was inferior to that of the control group during the retention phase of the experiment, $F(1,4) = 18.18$, $p < .05$.

Discussion

The results of Experiment 1 seem consistent with a sensory loss interpretation. Past work suggests that intact rats do attend to the visuospatial aspects of the light CS (Gillespie & Cooper, 1973). Moreover, it is possible to suppose that light intensity was the primary cue used in those studies where transoperative losses were not observed. Specifically, when a CR to a light CS has survived visual decortication (e.g., Marquis & Hilgard, 1936) animals have acquired the habit while under bodily-restraint with the head immobilized. Such procedures might encourage the use of intensity cues. In contrast, in the present CER paradigm, the use of a localized light source, and the lack of bodily restraint might encourage the use of spatial cues.

If the sensory loss interpretation of the CER impairment is appropriate, a CER established to intensity cues should show good sparing following visual decortication. Experiment 2 assessed this possibility.

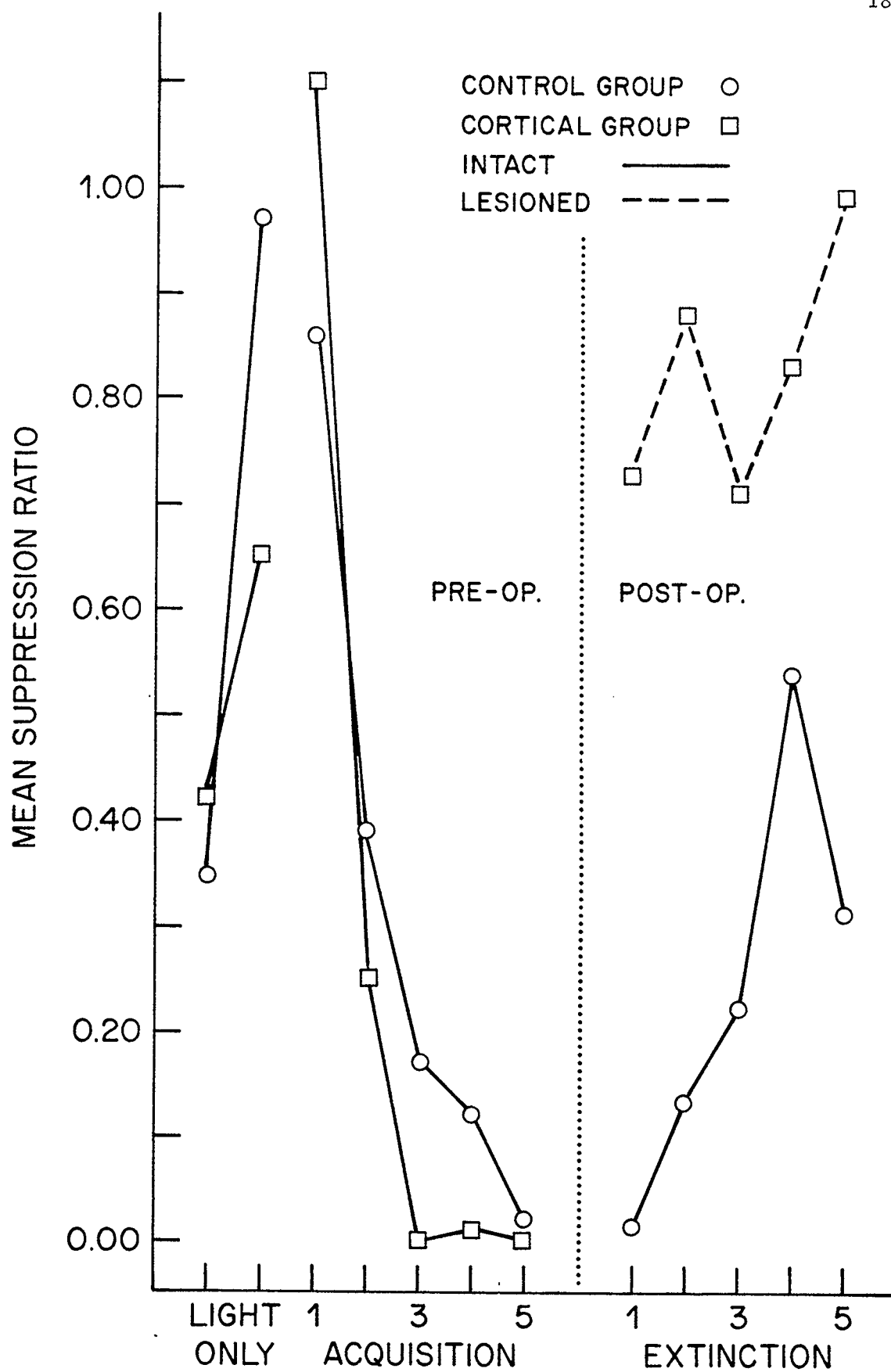


Figure 2. Experiment 1: The effects of large visual cortical lesions on a CER to a light CS.

CHAPTER III

EXPERIMENT 2

This experiment examined the nature of the transoperative CER impairment observed in Experiment 1.

Bauer and Cooper (1964), and Cooper et al. (1972) found that rats acquiring a two-choice, light-dark habit with light-diffusing occluders over their eyes show good sparing of the habit following large visual cortical lesions, while unoccluded rats do not. These researchers propose that unoccluded animals use spatial cues that are mediated by the cortical visual areas, while occluded rats use intensity cues that are mediated by subcortical visual areas. Thus, the differential effects of visual cortical lesions on the occluded and unoccluded two-choice, light-dark habits are attributable to the nature of the critical visual cue.

If the transoperative impairment observed in Experiment 1 is due to the use of spatial cues, rats acquiring the CER with occluders over their eyes should show more transoperative sparing of the habit than unoccluded rats. This possibility was assessed in Experiment 2.

Occluded and unoccluded rats acquired a CER to a light CS, then were subjected to large visual cortical lesions, and tested for retention of the habit. Since both occluded and unoccluded rats were lesioned a control for surgical trauma that was lacking in Experiment 1 was provided.

Method

Subjects

Twenty naive black-hooded rats, approximately 100 days old at the start of the experiment, were gradually reduced to 75% of their initial body weight, and maintained at this level throughout the experiment, except for rest and recovery periods, when weights were held at approximately 85%.

Apparatus

The apparatus consisted of five modified Behaviour Apparatus (Skinner) boxes enclosed in sound-attenuating cases. Fans provided a background noise level of about 60 db. The 1-min light CS a 24-V, 2.8-W lamp, mounted 8 cm above the lever, and 20 cm above the grid floor, emitted 12 ftc (123 lux) at source. Grason-Stadler E1064 shock generators were set at source to deliver the US, a .5-sec, .6-mA grid shock, at the end of the CS interval. Programming and recording equipment was located in an adjacent room.

Surgery

Surgical procedures were carried out with each animal under sodium pentobarbital anesthesia and secured in a Krieg stereotaxic instrument.

Post implantation. Following initial VI training, all 20 animals had an inverted T-shaped Teflon post fixed with stainless steel screws to the dorsal-anterior aspect of the skull. This post provided an anchor for .16-cm thick light-diffusing occluders or control head-pieces that were placed over each animal's eyes for each experimental session. To minimize the risk of infection at the implantation site,

1 ml of Penicillin G (300,000 I.U./ml) was given at the time of surgery, and .5 ml was given on the second and fourth day after surgery.

Visual cortical lesions. The surgical procedure that is detailed in Experiment 1 was used.

Procedure

Pretraining. The procedures employed in Experiment 1 were used to establish stable press rates on a VI 30-sec schedule. Following pretraining, all animals underwent surgery for a post implantation. After a five-day recovery period, the animals were given four more VI 30-sec training sessions. During this period, the animals were adapted to wearing occluders or the control headpieces. Assignment to either the occluded or unoccluded condition was then made, such that both groups had comparable VI press rates.

CER training. The training of the occluded and unoccluded groups was identical to that of Experiment 1 except that the US was a .6 mA shock and as the occluders reduced light intensity to about 1/6, the light CS was reduced by the same amount for the unoccluded group.

On the basis of CER acquisition performance the ten occluded and ten unoccluded animals were matched into four subgroups. One occluded and one unoccluded subgroup received large visual cortical lesions. At surgery one unoccluded and two occluded animals died. Two animals from the occluded control group were substituted for the lost occluded animals and received lesions.

After a 14-day rest and recovery period, the animals were returned to the Skinner boxes, and, following four VI sessions, tested for

retention of the CER. Again this test was one of extinction in that the CS presentations were not followed by shock during these five sessions.

Histology

Following the CER extinction test, the lesioned animals were heavily sedated with ether then perfused through the heart with physiological saline followed by 10% formalin. The brains were then removed, embedded in Parlodion, and sectioned at 40 microns. Sections throughout the extent of the LGN_d were mounted and stained with thionin.

Results

Anatomical

Gross inspection of the brains of the lesioned rats revealed that the cortical lesions were comparable to those made by Cooper et al. (1972) and Horel et al. (1966). Microscopic examination of the thionin-stained brain sections revealed extensive retrograde degeneration and gliosis throughout the extent of the LGN_d bilaterally. A detailed account as to the nature of LGN_d degeneration that ensues from visual cortical lesions is provided by Bland and Cooper (1970).

Behavioural

The data of the rats that died at surgery were discarded, and in Figure 3 the mean suppression ratios for the surviving members of the groups are presented.

Preoperatively, the occluded (n = 8) and unoccluded (n = 9) groups did not differ on initial exposure to the light, or throughout CER acquisition ($\bar{F} < 1.00$ in both cases). As Figure 3 illustrates, when

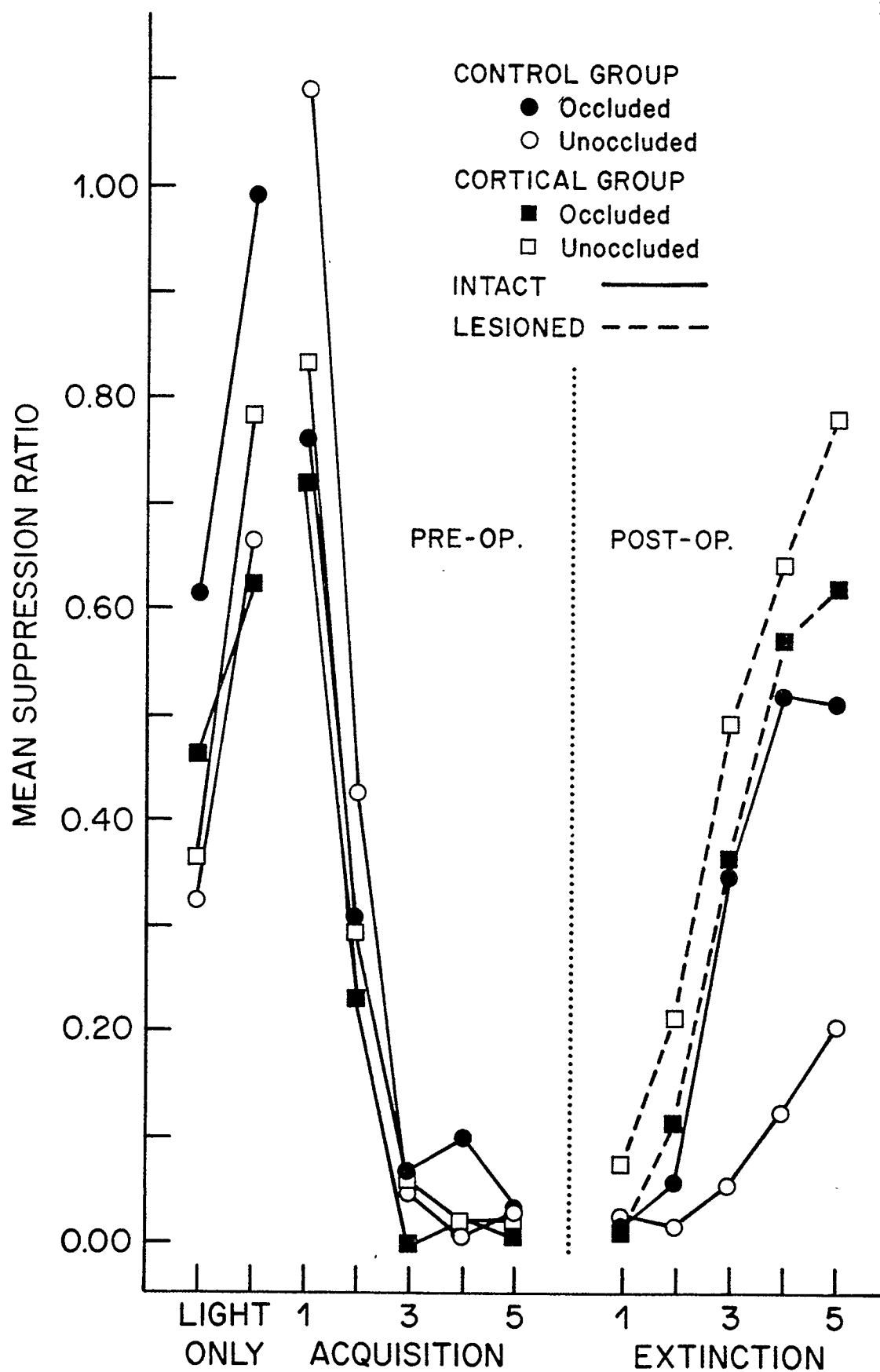


Figure 3. Experiment 2: The effects of large visual cortical lesions on an occluded and unoccluded CER to a light CS.

CER retention was assessed postoperatively during five extinction sessions, the unoccluded control group retained the CER better than the occluded control group. Hence, poor retention of the CER is evident only in the unoccluded cortical-lesion group. The occluded cortical-lesion group retained the CER as well as the unlesioned occluded control group. This differential lesion effect resulted in an occluded/unoccluded X lesion/control interaction that was marginally significant ($F(1, 12) = 4.20, p < .06$).

Discussion

This experiment showed that large visual cortical lesions impair an unoccluded CER habit more than an occluded CER habit. This differential lesion effect can be accounted for by supposing that the unoccluded habit is, at least in part, mediated by spatial cues that necessitate the involvement of visual cortex. Occluders by forcing reliance solely on intensity cues protect the habit from the effects of the visual cortical lesions as the intensity dimension of vision is mediated subcortically.

As the occluded cortical-lesion and occluded control groups showed comparable CER retention, it is unlikely that the CER impairment observed in Experiment 1 was entirely due to surgical trauma.

CHAPTER IV

EXPERIMENT 3

Experiment 2 showed that visual cortical lesions impaired the unoccluded CER habit more than the occluded CER habit. Thus, cortical lesions produce comparable effects in the CER situation and in the two-choice, light-dark, discrimination task where the animal is required to approach a lighted panel and avoid a darkened one.

In the two-choice, light-dark situation, lesions to one subcortical visual area, the pretectal region, produce effects that are opposite to those of visual cortical lesions. That is, pretectal lesions impair the occluded habit more than the unoccluded habit. Blochert et al. (1976) accounted for this differential lesion effect by supposing that the pretectal region subserves a critical visuosensory role in mediating intensity discriminations that are made by the occluded animal.

If the differential effects of pretectal lesions on the occluded and unoccluded light-dark habits are due to visuosensory factors, similar effects should be evident in the CER situation. That is, pretectal lesions should impair the occluded CER habit more than the unoccluded CER habit. Experiment 3 assessed this prediction. Occluded and unoccluded rats acquired a CER to a light CS then were subjected to pretectal lesions. Experiment 3 also included animals that were subjected to large visual cortical lesions as a check on the results of Experiment 2. Following postoperative retention testing, the occluded

and unoccluded pretectal animals, and the unoccluded animals with cortical lesions, were retrained to perform a CER to the light CS.

Method

Subjects

The subjects were 30 naive black-hooded rats that were approximately 100 days old at the start of the experiment. The deprivation procedure described in Experiment 1 was used.

Apparatus

The apparatus and programming equipment described in Experiment 2 was used, except that the positions of the lamp and lever were lowered, and a smaller, more easily manipulated lever substituted for the one used previously. These modifications, aimed at obtaining high, stable pressing on the VI 30-sec schedule, resulted in the lamp being located 9.5 cm above the lever, and 16.5 cm above the grids.

Surgery

Following initial VI training, all 30 animals had a post implanted on the anterior aspect of the skull. The surgical procedure described in Experiment 2 was used.

Visual cortical lesions. The procedure described in Experiment 1 was used. One occluded and one unoccluded animal died during surgery.

Pretectal lesions. An atlas of the rat's brain (König & Klippel, 1963) was used to provide target coordinates. A 1-mm diameter hole was drilled through the dorsal aspect of the skull in each hemisphere, at a point 3.5 mm posterior to bregma, and 1.5 mm lateral to the midline. A copper wire electrode, with the insulation removed from

the tip, was then lowered stereotaxically (Krieg instrument) to a point 5.5 mm below the skull surface, a placement estimated to be in the centre of the pretectal region. Using a Stoelting no. 58040 lesion device and a rectal anode to complete the circuit, electrolytic lesions were then made by applying a current of 2 mA for 60 sec. During surgery, one unoccluded animal died.

Procedure

Pretraining. The procedure described in Experiment 1 was used, except that an additional three sessions of VI training were given. All 30 animals then underwent surgery for a post implantation and, following a 24-day recovery period stable VI performance was reestablished and the animals adapted to wearing the experimental headgear. Assignment to either the occluded or unoccluded condition was then made, such that the groups had comparable VI press rates.

CER training. The rats were trained to perform a CER to a light CS using the procedure described in Experiment 1, except that a 2-min CS and a 1-mA shock were used and seven days of CER training were given to ensure adequate suppression to the light CS.

On the basis of their CER ratios, the occluded and unoccluded groups were divided, such that five occluded and five unoccluded animals received large visual cortical lesions, while five occluded and five unoccluded animals received pretectal lesions, and five occluded and five unoccluded animals served as unoperated controls. After surgery and an 18-day recovery period, the animals were returned to the Skinner boxes, and, following four VI sessions were tested for retention of the

CER during four extinction sessions.

The unoccluded visual cortical group and both the occluded and unoccluded pretectal groups were then retrained to perform a CER to the light CS.

Histology

The procedure described in Experiment 2 was used, except that the brains of the pretectal-lesioned animals were sectioned at 25 microns, and every fourth section was mounted and stained with thionin. These sections were light projected and mapped on the corresponding sections of a set of standard frontal diagrams derived from the König and Klippel (1963) rat brain atlas.

Results

Anatomical

Visual cortical lesions. Gross inspection of the brains of the cortically-lesioned rats indicated that the lesions were comparable in size to those of Experiment 2. Microscopic examination of thionin-stained sections from the brains of these rats indicated that extensive retrograde degeneration and gliosis were evident throughout the extent of the LGN_d bilaterally.

Pretectal lesions. Examination of the brain sections of the five occluded and four unoccluded animals revealed that the lesions were well placed within the pretectal region and comparable in extent to those made by Blochert et al. (1976).

Behavioural

The mean suppression ratios for each group are shown in Figure 4.

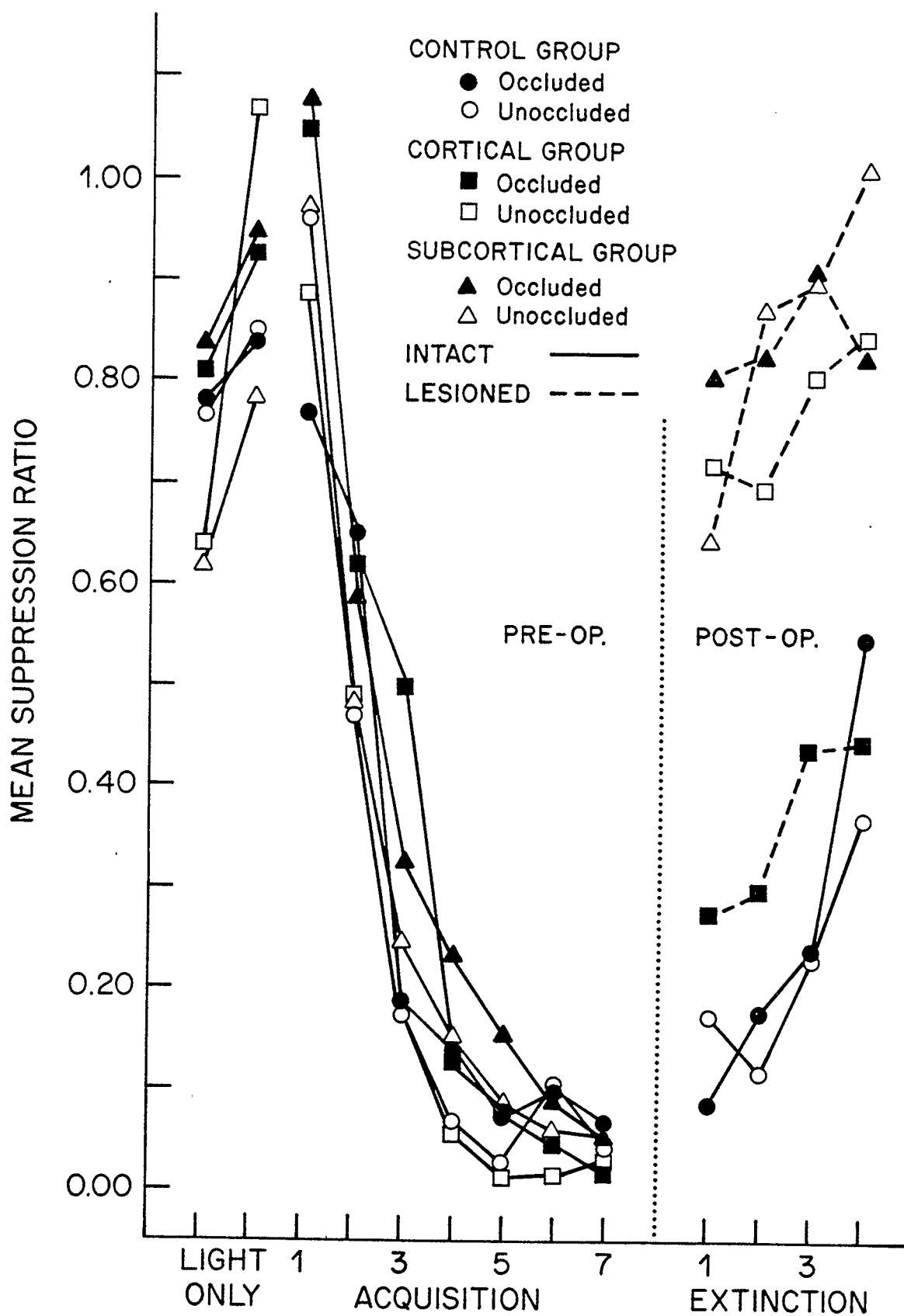


Figure 4. Experiment 3: The effects of large visual cortical lesions and subcortical lesions of the pretectal region on an occluded and unoccluded CER to a light CS.

Preoperatively, the occluded ($n = 14$) and unoccluded ($n = 13$) groups were similar during initial light exposure and CER training, $F < 1.00$, in both cases. Figure 4 illustrates that postoperatively the unoccluded visual cortical group was more impaired than the occluded visual cortical group, while both the occluded and unoccluded pretectal groups were impaired.

An analysis of extinction suppression ratios revealed a lesion/control effect, $F(2, 21) = 21.56$, $p < .01$. Planned comparisons made on the lesion/control X occluded/unoccluded interaction, showed that the visual cortical/control X occluded/unoccluded interaction was significant, $F(1, 21) = 4.37$, $p < .05$, while the pretectal/control X occluded/unoccluded interaction was not, $F < 1.00$.

As Figure 5 illustrates, CER retraining again failed to differentiate the two pretectal groups, $F < 1.00$. Both groups, however, had elevated suppression ratios when compared to the unoccluded visual cortical group that was also retrained.

Discussion

The present experiment complimented Experiment 2 by showing that large visual cortical lesions impaired the unoccluded CER habit more than the occluded CER habit. These differential effects are comparable to those observed in the two-choice, light-dark situation. Thus, further support is gained for the idea that the nature of the behaviourally effective cue determines whether cortical or subcortical visual areas subserve the predominant visuosensory role in a visually-guided habit.

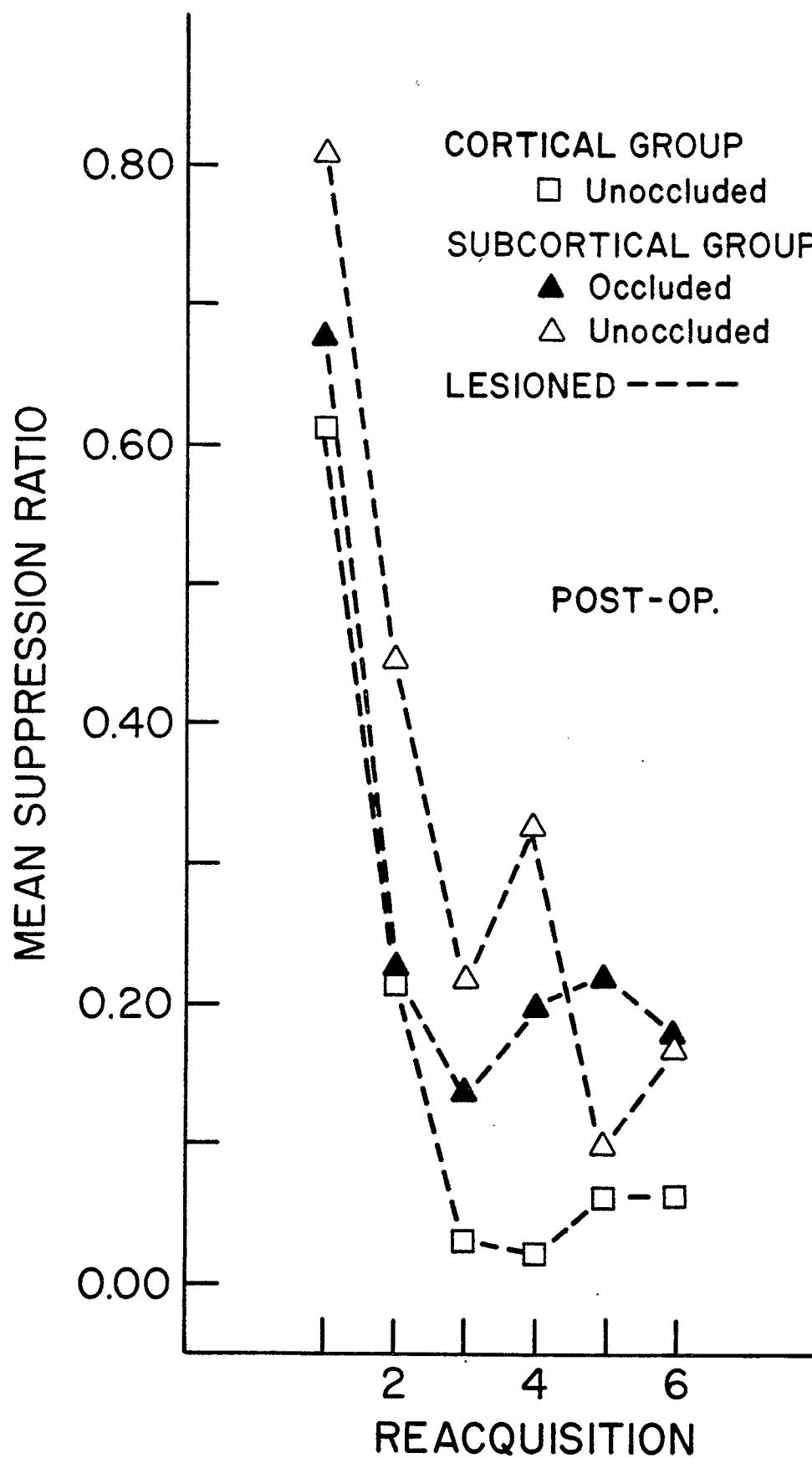


Figure 5. Experiment 3: Reacquisition of a CER to a light CS.

While the cortical data from the present experiment are consistent with the cue hypothesis, the subcortical pretectal findings are not, as both the occluded and unoccluded CER habits were impaired by lesions to this area. Moreover, when the animals with pretectal lesions were retrained to perform a CER to a light CS, again there was no indication that the occluded pretectal animals were handicapped more than the unoccluded pretectal subjects. These data are discrepant with those of Blochert et al. (1976) who found that pretectal lesions particularly impaired the two-choice occluded light-dark habit. They inferred that the pretectum subserves a critical visuosensory role in mediating light-intensity discriminations that are made by the occluded animal.

In the present experiment there were indications that pretectal lesions produce response acceleration. After being subjected to pretectal lesions, some animals barpressed on the VI schedule at rates that were considerably higher than those observed preoperatively. A particularly striking example of this was provided by a rat that accelerated from a rate of 50 presses per minute prior to surgery, to a rate of 116 per minute postoperatively. Such observations, and the difficulty both pretectal groups encountered in suppressing barpressing during postoperative CER training suggest that lesions in the vicinity of the pretectal region induce nonvisual impairments.

CHAPTER V

EXPERIMENT 4

In Experiment 3, animals acquired a CER to a light CS then were subjected to pretectal lesions. Upon being returned to the Skinner boxes, some of these animals pressed at rates that were considerably higher than those observed preoperatively.

Experiment 4 was a further assessment as to the effects of pretectal lesions on barpressing. Rats were given pretectal lesions then trained to barpress on a VI schedule.

MethodSubjects

The subjects were 25 naive, black-hooded rats that were approximately 100 days old at the start of the experiment. The animals were deprived using the procedure described in Experiment 1.

Apparatus

The apparatus described in Experiment 3 was used.

Surgery

Prior to barpress training, 15 animals received pretectal lesions using the procedure described in Experiment 3.

Procedure

Magazine and CRF training for the 15 pretectal and 10 intact control animals was carried out using the procedure described in Experiment 1. Six sessions of VI training were then given. During the first two

sessions a VI 15-sec reinforcement schedule was operative, then, for the next four sessions, a VI 30-sec schedule was in effect.

Histology

At the end of testing, the lesioned animals were sacrificed, and verification of lesion site was carried out using the procedure described in Experiment 3.

Results

Anatomical

Examination of the brain sections of the lesioned animals showed that the lesions were smaller than intended, and many of them coursed caudally into the superior colliculus.

Behavioural

As illustrated in Figure 6, over sessions the lesioned animals rapidly accelerated to barpress at higher rates than the intact control animals. A t -test performed on Day 3 rates showed that this difference was significant ($t(23) = 3.31, p < .01$).

Discussion

The results of Experiment 4 show that pretectal lesions elevate press rates on a VI schedule. Hence, they confirm the more informal observations of Experiment 3, and indicate that in the Skinner box situation one prominent effect of pretectal lesions is that of a nonvisual impairment.

Other researchers have noted that lesions to thalamic nuclei that are located medial and anterior to the pretectal region release checks on the frequency of certain behaviours. For example, Means, Harrell,

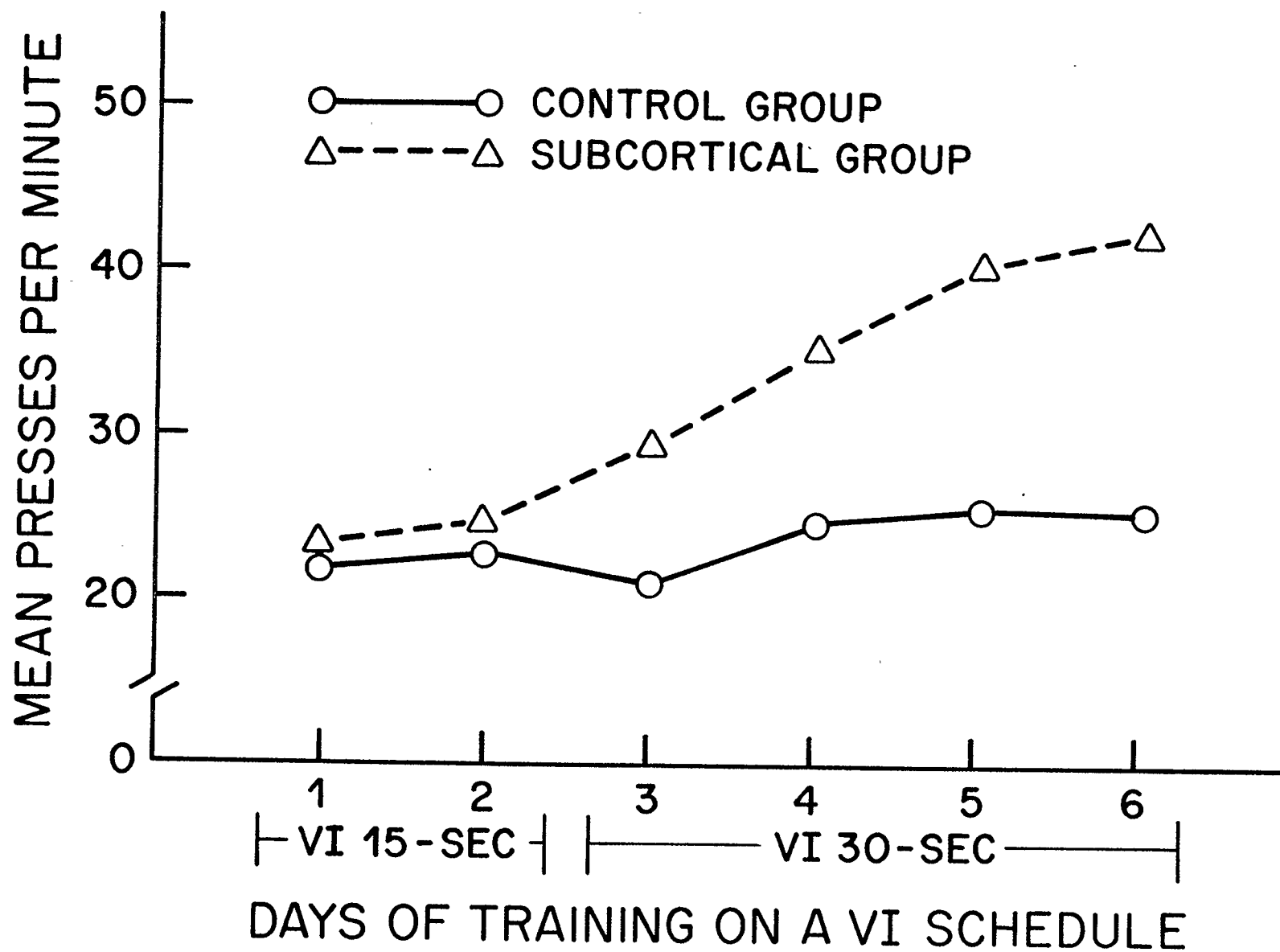


Figure 6. Experiment 4: VI press rates of animals with subcortical lesions and intact control animals.

Mayo and Alexander (1974) noted that rats with dorsal medial thalamic lesions displayed increased activity in a free exploratory situation and reduced spontaneous alternation in a T-maze. Means et al. suggested that these lesions retard the habituation of orienting responses. Rats with dorsal medial thalamic damage also barpress on VI schedules at rates that are considerably higher than those of intact animals (Dantzer & Delacour, 1972).

Dantzer and Delacour imply that rate acceleration on a VI schedule is specifically attributable to dorsal medial thalamic damage. The present findings counter this claim, however, as more caudally placed lesions produced a comparable effect. Indeed, the present data raise the possibility that lesions throughout this general subcortical area could be particularly deleterious to responses that have a strong inhibitory loading.

It would seem then that pretectal lesions impaired both the occluded and unoccluded CER habits in Experiment 3, because lesions to this subcortical area release a check on the CER baseline response of barpressing. Consequently, difficulties are encountered in stopping barpressing during the CS periods of CER training.

Conceivably then, the selective impairments that pretectal lesions induce in the two-choice, light-dark situation could be due to nonvisual response factors. That is, perhaps the occluded and unoccluded versions of this task have different response demands. Hence, pretectal lesions could selectively impair the occluded, two-choice, light-dark habit because of its particular response demands rather than its visuosensory aspects as Blochert et al. (1976) proposed.

CHAPTER VI

SUMMARY AND CONCLUSIONS

This study showed that large visual cortical lesions impair the unoccluded CER habit more than the occluded habit, while subcortical lesions equally impair both CER habits. Moreover, it was also observed that the subcortical lesions elevate VI rates of barpressing.

The effects of visual cortical lesions in the CER situation are consonant with those found in the two-choice, light-dark task (Bauer & Cooper, 1964; Cooper et al., 1972). Thus further support is provided for the idea that the cortical visual areas are more involved in mediating habits guided by spatial cues than they are in habits guided by intensity cues.

Subcortical lesions selectively impair the occluded version of the two-choice, light-dark habit. These same subcortical lesions, however, equally impair the performance of both the occluded and unoccluded CER habits, and induce higher barpress rates on a VI schedule. These findings made in the CER situation suggest an alternative to the Blochert et al. (1976) view that the pretectal region subserves a critical visuosensory role in mediating intensity discriminations.

According to this alternative interpretation, the occluded version of the simultaneous, light-dark habit places particular emphasis on the withholding of responses. This occurs because the occluded animal

can only make visual discriminations on the basis of successive changes in the intensity of a single diffuse array of light. For example, suppose on a given trial the occluded animal moves towards the left goal box. If light intensity progressively increases, it will continue in this direction and reach the positive lighted goal box. However, should light intensity decrease with this leftward motion, the animal must stop and keep redirecting its position until these movements bring about progressive increments in light intensity as the positive right goal box is approached.

This type of responding to a succession of light intensities over time would seem to necessitate a powerful "braking" mechanism, one, that according to the hypothesis under consideration, is disrupted by pretectal lesions. The impairment of the braking mechanism would be less detrimental to the unoccluded animal because the light stimulus, having a definite locus in space, is a more effective guide to the appropriate directional response required.

The proposed response interpretation is speculative, as the exact nature of the occluded, two-choice, light-dark response remains to be elucidated. Nonetheless, this line of speculation is supported by ongoing unpublished work from this laboratory. This work shows that subcortical lesions to the nonvisual anterior thalamus also selectively impair the occluded light-dark habit, and induce rate acceleration in a barpressing situation. Moreover, an unoccluded successive version (two lights, go right; no lights, go left) of the two-choice, light-dark task is severely impaired by pretectal lesions.

In conclusion, the present study indicates that subcortical lesions in the vicinity of the pretectal area particularly impair certain response mechanisms, and not the intensive aspect of vision as Blochert et al. (1976) proposed. It seems the response aspects of tasks such as the simultaneous, two-choice, light-dark task are changed by occlusion, while those of tasks already emphasizing the withholding of responses are not. Hence, it can no longer be assumed that occlusion induces a visuosensory change that necessarily leaves the learning demands of any given task constant to both occluded and unoccluded animals.

Finally, it would seem that conceptualizations as to the contributions of cortex and subcortex to visually-guided behaviour should consider both the visuosensory and response aspects of behaviour. Subcortical visual areas, for example, seem quite capable of mediating the more rudimentary aspects of vision along a continuum ranging from light intensity, devoid of spatial attributes, to crude spatial vision. Perhaps this occurs because such percepts are optimally keyed in to temporal go, no-go subcortical response mechanisms.

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