The role of the pretectum in the acquisition and retention of visual discrimination habits in monkeys

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Seven rhesus monkeys were trained to discriminate between each of three pairs of stimulus plaques, namely (1) black vs. white, (2) horizontal vs. vertical stripes, and (3) triangle vs. diamond. Six animals were then subjected to subcortical electrolytic lesions. The three subjects that received bilateral damage to the pretectal region exhibited a significant loss in the retention of the horizontal vs. vertical stripe discrimination as compared to normal or brain-operated controls. Subjects that sustained bilateral damage to the area immediately ventral to the pretectal region showed significantly poorer retention of the triangle vs. diamond task compared to the other subjects. In addition, monkeys with bilateral pretectal damage needed significantly more trials to learn a new visual discrimination task than the control group. The pretectal animals were not impaired relative to controls on the number of trials necessary to learn a 5-sec delayed alternation task. Possible functions of the pretectal region are discussed in light of the present results.

The pretectal region in primates is part of the vaguely defined zone located between the thalamus and midbrain (Scalia, 1972). It receives direct retinal input via the brachium of the superior colliculus (Giolli & Tigges, 1970; Hendrickson, Wilson, & Toyne, 1970), as well as projections from various visual cortical areas including the striate, prestriate, and inferotemporal cortices (OC, OB, OA, TE) (Campos-Ortega, Hayhow, & Cluver, 1970; Kuypers & Lawrence, 1967; Reitz & Pribram, 1969). Other cortical projections to the pretectal region have been reported from the frontal eye fields (FDF) (Astruc, 1971), the "prefrontal" and premotor cortex (FD, FB, FC, and FCBm) (Kuypers & Lawrence, 1967), and the parietal lobe (PE, PF, PG) (Petrus, 1971).

This region has been implicated in a variety of visual functions in monkeys. Magoun, Atlas, Hare, and Ranson (1936) reported that the pretectum is part of the pupillary light reflex pathway. More recently, Carpenter and Pierson (1972) demonstrated that only large lesions involving the posterior commissure and parts of central gray as well as the pretectal region significantly impair the pupillary light reflex. Other studies report that lesions in the pretectal region result in a variety of oculomotor deficiencies such as paralysis of downward gaze and optokinetic nystagmus (Pasik, Pasik, & Bender, 1969a, b). The conclusions concerning the role of the pretectal region presented in text books and other summary

statements usually limit it to such basic visual functions as those mentioned above. However, recent evidence indicates that the pretectal region is involved in more complex functions as well.

In their study on the effects of superior collicular ablations on higher visual functions, Anderson and Symmes (1969) inadvertently destroyed parts of the pretectal region in some subjects. Animals that received lesions destroying parts of the pretectum required extensive postoperative training before regaining criterion on pattern and color discriminations learned preoperatively, while those receiving lesions restricted to the superior colliculi did not. Flicker discrimination was essentially unimpaired in both groups. Thompson and Myers (1971) investigated the effects of various lesions to the brainstem on visually guided behavior in the rhesus monkey. Monkeys receiving lesions to the pretectal area or to the adjacent nucleus posterior thalami were significantly impaired in relearning a form and pattern problem but not a color discrimination. It is of interest to note that the pretectal region has also been reported to serve a critical function in the "visual memory system" of the white rat (Thompson, 1969) and in the acquisition of pattern discrimination habits in the cat (Berlucchi, Sprague, Levy, & DiBerardino, 1972).

The present study was designed to investigate the effects of selective subcortical destruction on the retention of visual discrimination habits learned preoperatively, and thus to attempt to corroborate the reports mentioned above (Anderson & Symmes, 1969; Thompson & Myers, 1971). In addition, the effects of such lesions on the acquisition of new visual and nonvisual problems were explored. Of particular interest was the role of the pretectum in visually

This report is based on a thesis submitted by the senior author to the University of Connecticut in partial fulfillment of the requirements for the MS degree. The research was supported by USPHS Grant MH-10972 to the second author. Please send reprint requests to William A. Wilson, Jr., Department of Psychology, U-20, University of Connecticut, Storrs, Connecticut 06268.

guided behavior. The establishment of the pretectum as a subcortical area that functions in the monkey's visual memory system will cast further doubt on the classical dichotomy between cortical and subcortical systems in visually guided behavior of primates.

METHOD

Subjects

Seven experimentally immature male rhesus monkeys (*Macaca mulatta*) were used as subjects. (An initial pilot study was conducted with three mature experimentally sophisticated monkeys; see Discussion, below.) The animals were individually housed with free access to water. They were fed Purina Monkey Chow once per day after testing. Their weights at time of surgery were between 3.2 and 4.1 kg.

Apparatus and Procedure

The subjects were tested in a modified Wisconsin General Test Apparatus (WGTA). The stimulus tray, located approximately 25 cm below the monkey's eye level, contained two foodwells spaced 10 cm apart. When the animal sat in the front of the restraining cage, the foodwells were within 10 cm of its reach.

Following pretraining, all animals were taught to discriminate between three pairs of stimulus objects (original learning, OL). The first pair consisted of square Masonite plaques, 57 x 57 x 3 mm, one painted black and the other painted white (problem BW). The monkeys were required to uncover the foodwell concealed by the black plaque in order to receive a 190-mg pellet. The white plaque covered an empty foodwell. In all discrimination tasks, the position of the positive plaque varied from left to right according to a Gellermann (1933) sequence. Monkeys were given 30 noncorrection trials per day, with a 10-sec interval between trials. Testing was usually conducted 5 days per week until a criterion of 27 correct responses in three consecutive blocks of 10 trials was reached.

Following completion of problem BW, monkeys were taught to choose a vertically oriented striped pattern and to avoid a horizontally oriented one (problem HV). These two stimuli and those for the three other problems described below were painted on square Masonite plaques, 56 x 56 x 6 mm. The striped stimuli consisted of three white stripes and three black stripes of approximately the same width. For the third preoperative problem, the monkeys were required to learn to choose a black equilateral triangle (39 mm on each side) and to avoid a black equilateral, equilateral diamond (90° angles, 25 mm on each side). The forms were of equal area, and each was painted on a white background (problem TD). Prior to surgery, two animals in each operated group (No. 12 and No. 14; No. 4 and No. 16) and the normal control (No. 13) were retrained to a criterion of nine correct responses in a block of 10 trials.

Five monkeys were subjected to bilateral subcortical lesions 6 to 8 weeks after completion of original learning. One other received its operation 2 weeks after completion of OL, while a seventh was left intact as a normal control. Following a postoperative recovery period of at least 2 weeks, all animals were required to relearn the three OL tasks in the same sequence as they were learned originally.

Two new tasks were then administered. The first was a discrimination problem using two identical stimulus plaques with a white semicircle (50-mm diam) centered on a black background (problem SC). The subjects were taught to choose the semicircle with the curved edge facing them and to avoid the semicircle with the straight edge closest to them.

Finally, animals were required to perform a spatial delayed-alternation task (problem ALT). For the first trial of a day, both foodwells were baited and covered with identical green square stimulus plaques. The monkeys were allowed to push aside either plaque in order to receive a food pellet. On each remaining trial, the side opposite the one chosen in the previous trial was baited, regardless of whether the previous trial had been correct or not.

Subjects were given 30 trials per day with 5 sec between trials. If a subject did not reach criterion in 600 trials, it was given 60 trials a day to a maximum of 2,000 trials.

Surgery and Histology

The monkeys were anesthetized with sodium pentobarbital (30 mg/kg intraperitoneally), and surgery was carried out under aseptic conditions. All lesions were bilateral and produced electrolytically in one stage, while monkeys were secured in a David Kopf Instruments stereotaxic holder. Stereotaxic coordinates for the pretectal region were determined utilizing the atlas of Snider and Lee (1961) with correction factors suggested by Thompson (Note 1) and Mishkin (Note 2). Lesions were made by passing a constant current (anodal in reference to an anal cathode) of 10 mA for 35 sec through an electrode made of 21-ga stainless steel hypodermic tubing coated with Thermobond (Sterling Varnish Co.) and with 2 mm of the sharpened tip exposed. Two penetrations were made in each hemisphere, and two lesions were produced with each penetration.

Upon completion of postoperative testing, the brain-operated animals were anesthetized with a lethal dose of sodium pentobarbital and perfused through the heart with normal saline followed by 10% Formalin. The brains were removed, blocked, and fixed in 10% Formalin, and later frozen and sectioned frontally at 60 and 90 microns. Two adjacent sections were taken every 0.5 mm through the lesion. One set of sections was stained for cells (cresyl-violet), while another set was photographed by passing light through the section onto Kodabromide F-5 enlarging paper and developing in the usual manner.

Subjects in the experimental group (Nos. 4, 10, 16) sustained bilateral damage to the pretectal region with varying amounts of damage to adjacent structures. These structures included the superior colliculus, nucleus limitans, habenula, central gray, nucleus parafascicularis, and/or the nucleus magnocellularis of the commissura posterior. Figure 1 represents lesions sustained by each subject copied from brain sections at the level of the posterior commissure.

The three operated subjects in the control group (Nos. 8, 12, 14) sustained brain damage which was equal to or greater than the amount of damage incurred by the experimental group (see Figure 1). The areas of destruction included the superior colliculus, pulvinar, nucleus limitans, habenula, central gray, nucleus

Figure 1. Coronal sections of lesions at the level of the posterior commissure. Each section is labeled with subject's number. Darkened areas indicate regions of tissue degeneration or destruction. Structures are labeled as follows: cc, corpus collosum; ch, commissura habenularis; gc, central gray; hm, medial habenula; hp, hippocampus; lgn, lateral geniculate nucleus; np, nucleus pontis. Arrows indicate intact pretectal region.

Table 1
Trials to Criterion for Each Task

Groups	Monkey No.	Preoperative			Postoperative			Postoperative Acquisition	
		B-W	H-V	T-D	B-W	H-V	T-D	SC	ALT
Pretectal Operates	4	30	130	470	0	50	80	410	2000
	10	150	100	240	0	70	10	290	780
	16	50	230	220	80	200	220	370	800
Operated Controls	8	10	120	350	0	0	0	230	2000
	12	20	80	100	0	0	140	260	500
	14	10	90	410	0	0	10		
Normal Control	13	30	80	420	0	30	20	260	2000

parafascicularis, and/or the region immediately ventral to the pretectal region. One control subject (No. 14) sustained unilateral pretectal destruction as well as other brain damage, but none of the controls received bilateral pretectal lesions.

RESULTS

Table 1 shows the numbers of trials to criterion for each subject for all tasks; error scores followed the same general pattern throughout. All but one animal exhibited perfect retention of problem BW. Monkey No. 16, which sustained the most extensive damage to the pretectal region, showed a severe loss (-60% savings), requiring more trials to relearn the task than it needed to learn it initially. (Savings scores for postoperative retention were calculated by subtracting post operative trials to criterion from preoperative trials to criterion and then dividing this remainder by the number of preoperative trials to criterion.)

Subjects that sustained bilateral damage to the pretectal region had significantly poorer retention of problem HV than did the control group (Mann-Whitney $U = 0$, $p = .03$, one-tailed test). Their savings scores were 62%, 30%, and 13%. The three operated controls had perfect retention of problem HV, while the normal control had a savings score of 63%.

When animals with bilateral damage to the pretectal region were compared to the control group, there was no significant difference in retention of problem TD between the two groups. However, it may be noted that the two animals that sustained bilateral damage to the region immediately ventral to the pretectal region (Nos. 12, 16) showed significantly poorer retention (-40% and 0% savings, respectively) than the remaining five subjects ($U = 0$, $p = .05$, two-tailed test), which had essentially perfect retention.

One control animal (No. 14) died before the postoperative acquisition phase of the experiment. Monkeys in the experimental group with bilateral pretectal damage took significantly more trials to learn the novel visual discrimination task,

problem SC, than monkeys in the control group ($U = 0$, $p = .05$, one-tailed test).

No significant difference in the number of trials to criterion was found between control and experimental animals on the delayed alternation task (problem ALT). Two control animals and one experimental failed to learn the problem after 2,000 trials. Their scores were only slightly better than chance at completion of testing.

It should be noted that monkey No. 16 exhibited disturbances of gaze and body posture, such as head hyperextension and paralysis of downward gaze. These are components of the pretectal syndrome described by Pasik et al. (1969a). The other two experimental subjects did not exhibit this syndrome, presumably due to the fact that the lesions incurred by these animals spared the crucial interstitial nuclei of the posterior commissure (see Pasik et al., 1969a).

One operated control animal (No. 12) exhibited partial paralysis of both legs after surgery, which necessitated propping up the animal in the testing cage. This dysfunction did not impair the subject's ability to reach the stimulus plaques.

DISCUSSION

The present study supports previous reports of visual retention deficits following bilateral pretectal destruction in monkeys (Anderson & Symmes, 1969; Thompson & Myers, 1971). In addition, monkeys with bilateral pretectal damage were deficient in learning a new visual discrimination task, but they did not differ from controls in their ability to learn a nonvisual alternation task.

The monkey with the most extensive damage to the pretectal region (No. 16) showed the most severe loss in retention on all three problems. The only significant loss exhibited by the two other pretectal operates was on problem HV. It should be noted that despite disturbances in gaze and body posture, monkey No. 16 was observed to reach out accurately for the stimuli and to move its head in such a fashion that it could direct its eyes at the stimuli.

Two animals (No. 12 and one of the pilot subjects) received lesions that damaged the area immediately ventral to the pretectal region without extending into the pretectum. These subjects showed a different pattern of retention loss than the experimental group discussed previously, exhibiting a severe loss on the form problem (problem TD) with little or no loss on the other two problems. Monkey No. 16, discussed above, received a lesion that destroyed both the pretectal region as well as the area just ventral to it. It showed a severe loss on the form problem (TD) as well as the pattern (HV) and black-white (BW) discrimination.

This suggested dissociation of function between these different regions of the mesodiencephalic junction is difficult to account for, given the present state of anatomical knowledge of this area. The area of the mesodiencephalic junction ventral to the pretectal region includes the nucleus posterior thalami (Kuhlenbeck & Miller, 1949) and the nucleus magnocellularis commissurae posterior (Snider & Lee, 1961). These nuclei have been included as part of the pretectal area by many anatomists (Atlas & Ingram, 1937; Kuhlenbeck & Miller, 1949; Scalia, 1972). The possible existence of different connections for each of these nuclei of the pretectal area with other cortical and subcortical areas may account for the role that each of these nuclei seems to play in the retention of form and pattern discriminations. It is of interest to note that Giolli, Towns, and Haste (1974) have demonstrated two distinct systems of fibers arising from visual cortex in rabbit which innervate the pretectal region.

The present study, as well as previous evidence, indicates the importance of the pretectal area in visually guided behavior in rhesus monkeys. With the limited data available, it is not possible to assess the extent or permanence of the impairment. In the present study, the subject with the most extensive damage showed severe retention losses but it was able to relearn the problems. Thompson and Myers (1971) reported that with extensive and possibly total destruction of the pretectal region, form and pattern discriminations could not be relearned in eight times the number of trials needed to learn the task preoperatively. In the formation and maintenance of a visual habit, the pretectum may be necessary to process information before it reaches the striate cortex, via direct retino-pretectal inputs, or after it is processed through the visual cortex, via striate-pretectal and inferotemporal-pretectal projections, or it may serve both functions.

The Pasiks have demonstrated that the accessory optic system (AOS) is a critical structure in extrageniculostriate vision, since its destruction in a destriate monkey abolishes even those discriminations that are based on total luminous flux. Yet, destruction of the AOS in the otherwise intact monkey

has no effect on visual discrimination performance (Pasik & Pasik, 1968, 1973). Destruction of the lateral pretectum in destriate animals results in a loss similar to that following AOS destruction (Pasik & Pasik, 1973), but, as this study demonstrates, destruction of the pretectal region in the intact monkey also significantly disrupts visual discrimination functioning. Therefore, it would appear that, unlike the AOS, the pretectal region is critical for normal visual performance in the intact as well as in the destriate monkey.

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(Received for publication January 6, 1975;
revision accepted July 9, 1975.)