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Pulvinar lesions in monkeys produce abnormal eye movements during visual discrimination training

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The pulvinar nucleus is perhaps the most enigmatic structure in the diencephalon. In man and monkey it occupies the posterior pole of the thalamus and is larger than any other thalamic nucleus. Presumably, its importance is somewhat proportional to its size; and yet, its function remains obscure since damage to the pulvinar rarely produces a discernable behavioral effect.

Since neurons in the pulvinar have visual receptive fields[1,22], it is likely that the pulvinar mediates a visual function. However, the results of numerous behavioral studies have shown that monkeys with pulvinar lesions perform normally on a variety of visual discrimination tasks[12,24,37] (for exceptions, see refs. 10 and 34). This is particularly puzzling since there are extensive reciprocal connections between the pulvinar and cortical areas involved in higher levels of visual processing, namely striate[5–9,20,23,27,28,35], prestriate[6–9,11,15,16,18,23,35,40] and inferior temporal cortex[11, 16,18,19,33,35,38]. But, the pulvinar also receives a strong projection from the superficial layers of the superior colliculus[4,21,24,36], and the role of the pulvinar in vision may be more closely related to its interaction with the colliculus than to its interaction with the cortex. For example, pulvinar lesions, like collicular lesions, may produce oculomotor impairments[17,25,32,41,42]. To investigate this possibility, we have examined the eye movements of monkeys with pulvinar lesions and compared them with those of normal monkeys during acquisition of a visual pattern discrimination problem.

The experimental procedure was as follows. At least 4 months prior to testing, 4 rhesus monkeys (*Macaca mulatta*) received bilateral pulvinar lesions. The lesions were produced by passing radio frequency current through stereotaxically placed electrodes (see ref. 37). The histological findings are presented in Fig. 1. In all 4 monkeys the lesions were extensive, but subtotal, in all cases sparing the anterior portion of the nucleus. However, in two of the 4 monkeys (P-G17 and P-G19) the caudal extent of pulvinar lateralis and pulvinar inferior was completely destroyed; this portion of the

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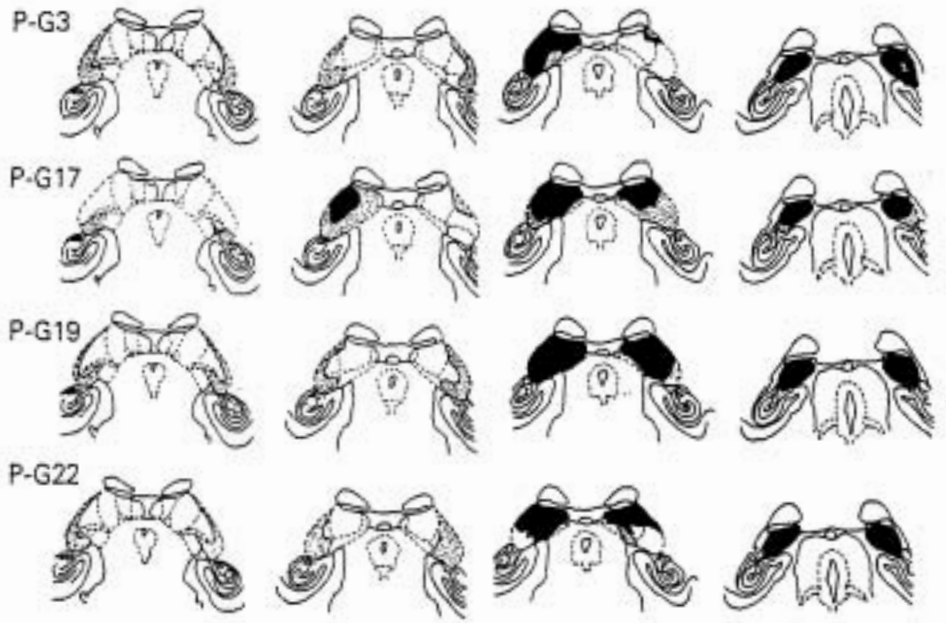

Fig. 1. Pulvinar lesions of individual monkeys in group P plotted onto coronal sections of a standard monkey brain (courtesy of H. E. Rosvold); coronal sections are at stereotaxic coordinates of AP + 2.0, + 1.0, 0.0 and −1.0. Blackened areas indicate the lesion; stippled areas indicate complete cell loss and dense gliosis.

pulvinar has anatomical connections with both cortical and subcortical visual structures[4–6]. In addition to pulvinar damage, passage of the electrode consistently produced minimal bilateral damage to the fornix and corpus callosum. There was no detectable damage to either the pretectal region or the superior colliculus, although the lesion did encroach on the brachium of the colliculus in all animals.

The 4 operated monkeys (group P) and 4 normal control monkeys (group N) were initially trained to position their right eye in the viewing port of a test chamber and scan a black and white photograph of a rhesus monkey face in order to obtain a banana pellet reward. When the monkeys had learned to consistently look through the viewing port for periods of 5 sec, formal discrimination training was begun. During discrimination training the eye movements of the monkeys were continuously monitored and simultaneously recorded on video tape using the Mackworth corneal reflection technique[2].

Discrimination training consisted of 4 consecutive days of testing in which monkeys were rewarded for fixating the letter 'P' in a stimulus display containing a 'P' and an 'R' (see ref. 3). The stimuli, which were rear-projected on a screen (25 × 25 cm) placed 38 cm from the viewing port, measured 6.35 × 6.35 cm (9.5° × 9.5° visual angle) and appeared as white letters on an opaque black background. They were positioned diagonally from each other and appeared with equal frequency in each quadrant of the display during a daily 40-trial test session. The quadrant position of the two stimuli varied randomly from trial to trial.

During each trial we observed the monkey's eye on a video monitor and

delivered a reward when the animal fixated the positive stimulus ('P'), that is, when the reflected image of the 'P' appeared on the animal's cornea at the center of his pupil. Delivery of the reward and closure of a shutter placed in front of the viewing port terminated the trial, which was followed by a 30-sec intertrial interval. On successive days we attempted to increase the length of fixation of the positive stimulus by withholding rewards until fixations of increasingly long duration were maintained.

Subsequent to completion of the 4 days of discrimination training, a trial-by-trial analysis was made of the video tape records for day 1 and day 4. The monkey's point of fixation on the stimulus display was determined at 200-msec intervals using a semi-automated computer graphics system which located the center of the pupil relative to the corneal reflection of the stimulus display.

A comparison of the eye movements of monkeys in groups P and N revealed several important findings:

(i) Pulvinar lesions did not affect discrimination learning based on preferential fixation of a visual stimulus; monkeys in group P acquired the pattern discrimination as easily as monkeys in group N. Data in Fig. 2 indicate that on day 1 neither group preferentially fixated either of the two stimuli, whereas on day 4 both groups preferentially fixated the positive stimulus ('P'). Visual fixations of the 'P' increased from day 1 to day 4 for all animals in both group P ($P = 0.062$) and group N ($P = 0.062$). Preferential fixation of the 'P' on day 4 was not significantly different between the two groups ($U = 4$, $P = 0.342$; Mann–Whitney U Test, two-tailed).

(ii) Nevertheless, removal of the pulvinar did influence visual behavior; in contrast to normal monkeys, monkeys in group P restricted most of their scanning of the visual display to the quadrants containing the stimuli. Data in Fig. 3 show that on day 1 normal monkeys gazed at the stimuli 51% of the time; that is, their fixations were distributed approximately equally between blank quadrants and those containing the stimuli. By comparison, monkeys in group P looked at the stimuli 70% of the time on day 1, significantly more than normal monkeys ($U = 0$, $P = 0.028$). By day 4 of visual discrimination training all animals in both groups had increased their attention

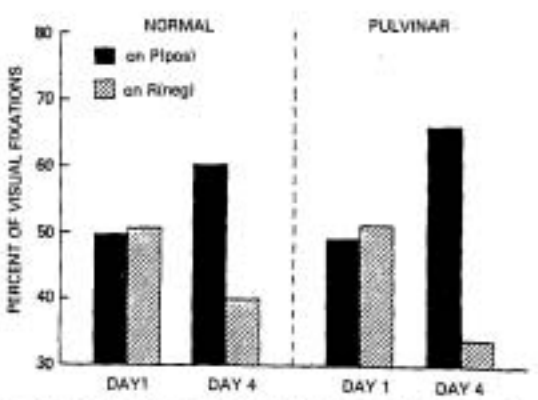

Fig. 2. Distribution of on-stimulus visual fixations directed to the positive ('P') and negative ('R') stimuli on days 1 and 4 of discrimination training for monkeys with pulvinar lesions (group P) and for normal control monkeys (group N).

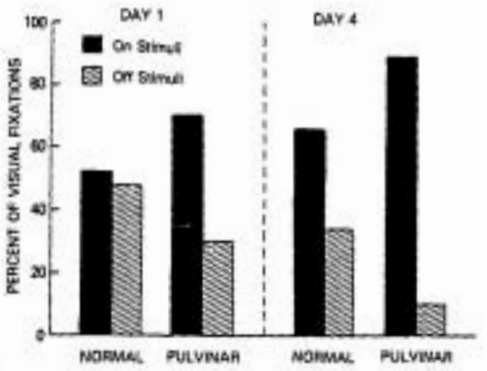

Fig. 3. Distribution of fixations on quadrants of the visual display with and without stimuli on days 1 and 4 of discrimination training for monkeys with pulvinar lesions (group P) and for normal control monkeys (group N).

to the stimuli, especially to the positive stimulus. Yet, on day 4 monkeys in group P fixated the stimuli 90% of the time, significantly more than normal monkeys who fixated the stimuli 63% of the time ($U = 0$, $P = 0.028$).

(iii) Pulvinar lesions produced a second type of eye-movement abnormality; the visual fixations of monkeys in group P were abnormally prolonged. Data in Fig. 4 reveal that the fixations of monkeys with pulvinar lesions were significantly longer than those of normal monkeys when the animals viewed quadrants of the display containing the stimuli; this was true on both day 1 ($U = 0$, $P = 0.028$) and day 4 ($U = 1$, $P = 0.056$). The mean duration of on-stimulus fixations for group P was over 450 msec longer than the mean for group N. As noted above, almost all of the fixations of monkeys in group P were directed to those quadrants of the display containing the stimuli. Yet, on day 1 even those fixations that were directed to blank quadrants were also abnormally prolonged ($U = 0$, $P = 0.028$). Prolonged staring at blank quadrants by monkeys in group P relative to group N disappeared by day 4 ($U = 6$, $P = 0.686$).

(iv) Damage to the pulvinar did not produce any other detectable eye-movement impairment. The results of neurological tests indicated that horizontal optokinetic

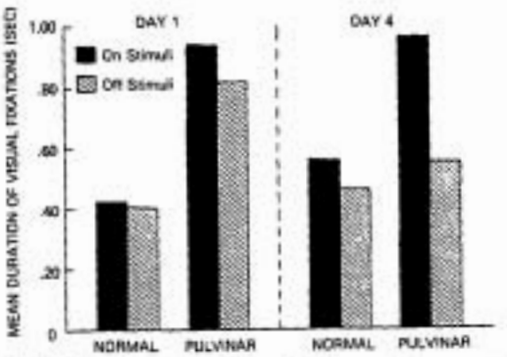

Fig. 4. Mean duration of visual fixations (sec) on and off the stimuli on days 1 and 4 of discrimination training for monkeys with pulvinar lesions (group P) and for normal control monkeys (group N).

nystagmus, convergence, vertical and horizontal saccades, and visual pursuit were all normal in monkeys with pulvinar lesions; although quantitative measurements were not made, eye-movement velocities appeared normal as well. Finally, there were no changes in pupillary reflexes, rate of blinking, or body posture following pulvinar surgery.

In summary, monkeys with pulvinar lesions were unimpaired in acquiring a visual discrimination, substantiating earlier findings[12,24,37]. However, during discrimination training their eye movements were abnormal in two respects. First, these monkeys displayed a paucity of saccades to blank portions of the visual field; that is, they appeared to be 'visually captured' by the stimuli. Second, their fixations were abnormally prolonged*.

The prolonged fixations observed in monkeys with pulvinar lesions are reminiscent of the oculomotor impairments which follow lesions of the primate superior colliculus. These include an increased latency to shift fixation to a peripheral target[25,32,41,42] and the more extreme case of fixed gaze[17]. However, the effects produced by the pulvinar lesions cannot be explained by inadvertent damage to the superior colliculus. Although the lesions in all 4 monkeys encroached on the brachium of the colliculus (Fig. 1), the monkeys who demonstrated the most prolonged fixations (P-G17 and P-G19) were the ones who sustained the most extensive damage, not to the brachium, but rather to the caudal portion of the pulvinar. Moreover, the prolonged fixations demonstrated by monkeys with pulvinar lesions do not reflect an impairment in oculomotor control. On day 1 of testing approximately 20% of the on-stimulus fixations of monkeys in group P lasted only 200 msec; in addition, by day 4 of testing their fixations on blank quadrants of the display were of normal duration. Thus, although monkeys with pulvinar lesions do not typically move their eyes rapidly, they are indeed capable of doing so. This is qualitatively different from the eye movements of monkeys with lesions of the superior colliculus, whose saccadic latencies are never normal, even after 40 days of extensive postoperative training[42].

Considering recent electrophysiological findings, it is not surprising that pulvinar lesions produce eye-movement abnormalities. There are single cells in the primate pulvinar which respond to both eye movements and light flashes[30], suggesting that the pulvinar nucleus is involved in processing aspects of both oculomotor and visual information. Damage to the pulvinar may disrupt such processing, and thereby result in visual capture and prolonged fixations. Visual capture has previously been

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* Oscar-Berman et al.[29] observed prolonged fixations in monkeys with foveal prestriate lesions and in those with inferior temporal lesions during visual discrimination learning. However, those animals stare only at the preferred stimulus, whereas monkeys with pulvinar lesions stare at both the positive and negative stimuli as well as at blank portions of the display. Moreover, the effect is less pronounced in monkeys with cortical lesions. The mean fixation duration (on the preferred stimulus) was 530 msec for monkeys with foveal prestriate lesions and 480 msec for those with inferior temporal lesions; by contrast, we observed a mean fixation duration (on both stimuli) of 940 msec for monkeys with pulvinar lesions. Recently, we have confirmed that the fixations of monkeys with foveal prestriate or inferior temporal lesions are abnormally prolonged[13]. A detailed report comparing the eye movements of monkeys with these cortical lesions to those of monkeys with pulvinar lesions during visual discrimination training is provided elsewhere[14].

interpreted as an indication of limited processing capacity, inasmuch as it is characteristic of human infants[31] and retardates[26,39]. Prolonged fixations may reflect an adaptive attempt by the animal to overcome such a processing deficit. The results of visual discrimination experiments are consistent with this hypothesis. Monkeys with pulvinar lesions successfully acquire visual discriminations under standard testing procedures with trials of unlimited viewing time[12,24,37], a situation which does not interfere with prolonged fixations. However, such monkeys fail to learn visual discriminations when the stimuli are flashed very briefly[10]; this manner of testing should greatly disrupt discrimination learning in animals who require prolonged fixations in order to adequately process visual stimuli. We are now attempting to elucidate the effect of pulvinar lesions on visual information processing by examining the eye movements of monkeys with these lesions as they scan complex visual arrays.

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