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PULVINAR LESIONS IN MONKEYS PRODUCE ABNORMAL SCANNING OF A COMPLEX VISUAL ARRAY

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Abstract—Eye movements of normal monkeys and monkeys with pulvinar lesions were recorded on video tape as the animals spontaneously scanned a complex stimulus array. During the test session, color was added to one stimulus in the array. Although monkeys with pulvinar lesions were not impaired in either visual orientation or habituation to this novel stimulus, their eye movements were abnormal in two ways. First, they appeared visually captured by the stimuli, making few saccades off the array. Second, their fixations were abnormally prolonged. These eye-movement abnormalities appeared to be associated with a disorder in visual processing rather than an impairment in oculomotor control.

THERE is strong evidence from both anatomical and electrophysiological studies that the pulvinar nucleus in primates mediates some aspect of visual function (for a recent review, see [1]). However, the results of behavioral studies have provided little information regarding the nature of this function. Despite extensive reciprocal connections between the pulvinar and cortical areas involved in higher levels of visual processing, i.e. striate [2-10], prestriate [3-6, 8, 11-16], and inferior temporal cortex [11, 13-15, 17-19], monkeys with pulvinar lesions perform normally on a variety of visual discrimination tasks [20-22]. Since the pulvinar receives additional input from the superficial layers of the superior colliculus [21, 23-26], damage to the pulvinar may instead produce oculomotor impairments similar to those described in monkeys with collicular lesions [27-33]. Indeed, there are neurons in the pulvinar which respond not only to visual stimuli [34-37], but to eye movements as well [38].

Recently we reported an analysis of both the oculomotor function and the discrimination capability of monkeys with pulvinar lesions [39]. Although these monkeys were unimpaired in learning the visual discrimination problem, they demonstrated two eye-movement abnormalities. Unlike normal monkeys, monkeys with pulvinar lesions appeared visually captured by the stimuli, showing a paucity of saccades to blank areas of the display. In addition, their fixations were abnormally prolonged, nearly 500 msec longer than those of normal monkeys. These abnormalities appeared to be related to a disorder in visual processing associated with discrimination learning rather than to an oculomotor impairment.

The purpose of the present study was to determine whether monkeys with pulvinar lesions would demonstrate eye-movement abnormalities when they *spontaneously* viewed visual stimuli. Spontaneous viewing was studied in a paradigm in which visual orientation and habituation could also be examined (see [40] and [41]).

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METHOD

Subjects

The subjects were eight young adult rhesus monkeys (*Macaca mulatta*) of both sexes, weighing from 4 to 6 kg at the time of surgery. Four of these monkeys had bilateral lesions of the pulvinar nucleus (Group P) and four were unoperated controls (Group N). All subjects were the same as those who participated in the visual discrimination experiment previously reported [39].

Brain surgery and histology

All monkeys in Group P underwent surgery at least 4 months prior to behavioral testing. Pulvinar lesions were produced by passing radio frequency current through stereotaxically placed electrodes. Complete details of surgical and histological procedures are reported elsewhere [22].

Pulvinar lesions of individual animals, plotted onto standard coronal sections of a normal monkey brain, are presented in Fig. 1. The lesions in all four monkeys were extensive, but subtotal, in all cases sparing the

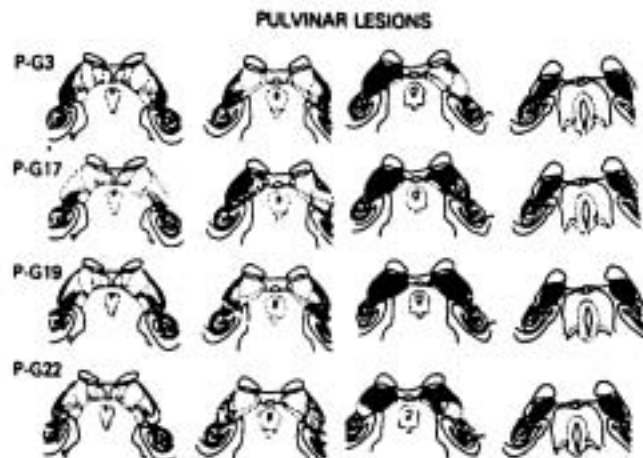


FIG. 1. Pulvinar lesions of individual monkeys plotted onto coronal sections of a standard monkey brain. Coronal sections are at stereotaxic coordinates of AP - 2.0, - 1.0, 0.0 and - 1.0. Blackened areas indicate the lesion; stippled areas indicate complete cell loss and dense gliosis. Actual tracings of coronal sections through the thalamus of each monkey with pulvinar damage are published elsewhere [42].

anterior portion of the nucleus. However, in two of the monkeys (P-G17 and P-G19) the caudal extent of pulvinar lateralis and pulvinar inferior was completely destroyed. 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.

Apparatus

Eye movements of monkeys were recorded using the Mackworth corneal reflection technique [43]. Details of the adaptation of the apparatus for recording eye movements of unrestrained monkeys are reported elsewhere [44]. In the present experiment, the monkey viewed stimuli through the eye port of a test chamber equipped with an electronically controlled shutter. The stimuli were rear-projected onto a transparent display screen (25 cm x 25 cm) placed 38 cm from the eye port. A half-silvered mirror was placed at a 45° angle between the eye port and the stimulus display. A television camera with a telephoto lens was positioned at the side of the test chamber, 90° from the animal's line of sight; it was focused upon the half-silvered mirror and recorded the image of the monkey's eye with the reflection of the stimulus display upon the cornea. The output of the camera was continuously monitored during test sessions and stored on video tape for subsequent data analysis.

Procedure

Prior to testing, all operated and normal monkeys were trained to position one eye in the eye port of the test chamber and scan a photograph of a monkey face. The stimulus array used during testing consisted of 16 geometric figures; each figure measured 4.5 cm × 4.5 cm (6.75° visual angle). The array was presented for 5-sec trials with a 30-sec intertrial interval, 40 trials per day, on two consecutive days. Monkeys were rewarded with a single banana pellet at the end of each trial. At no time during testing were rewards given for selective patterns of scanning.

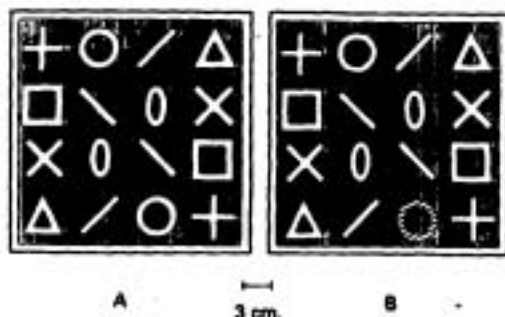


FIG. 2. Stimulus arrays used in the present study. A was presented on trials 1-10 and 31-40 of each day's session; B was presented on trials 11-30. The circle with the slanted lines in B is the stimulus which was colored red on day 1 of testing; on day 2, the circle in the top line of the array was colored red.

On the first and last 10 trials of each day's session, all of the 16 figures within the array appeared as white stimuli on a black background, as shown in Fig. 2(A). On the middle 20 trials of each day's session, a single figure within the array was colored red, as shown in Fig. 2(B). Visual orientation and habituation to this novel stimulus were recorded by video taping eye movements as the monkey scanned the stimulus array.

Video tape and data analysis

Upon completion of behavioral testing, a trial-by-trial analysis of the video tape records was made. For each trial, the monkey's point of fixation on the stimulus display was determined at 200-msec intervals using a semiautomated computer graphics system. The technique for determining the point of fixation was as follows. Two computer-generated right angle cursors and a circular cursor of adjustable diameter were superimposed on stopped frames of the video tape. An observer precisely positioned the circular cursor over the image of the monkey's pupil and positioned the right angle cursors over the corneal reflections of the bottom corners of the stimulus display. The cursor coordinates for every sixth frame were scored in this manner and were stored in digital form on magnetic tape. Subsequently, the coordinate data from these scored frames were integrated with information regarding the position of the stimuli within the display, thereby determining at 200-msec intervals the monkey's point of fixation on the display. The resolution of the eye-movement system, which was approximately $\pm 2^\circ$ of visual angle, was well within the accuracy required for discriminating between fixations made among the stimulus figures within the display.

Mann-Whitney *U* tests (two-tailed) were employed to test for significant differences between Groups P and N. Within group comparisons were made using the *t* test for related means (two-tailed). All tests were performed on the combined data from the 2 days of testing.

RESULTS

Visual orientation and habituation

A comparison of the visual fixations of monkeys in Group P with those in Group N revealed that pulvinar lesions did not affect either visual orientation or habituation to the novel stimulus. Data in Fig. 3 indicate that both normal monkeys and those with pulvinar lesions oriented to novelty by shifting their gaze toward the stimulus to which color was

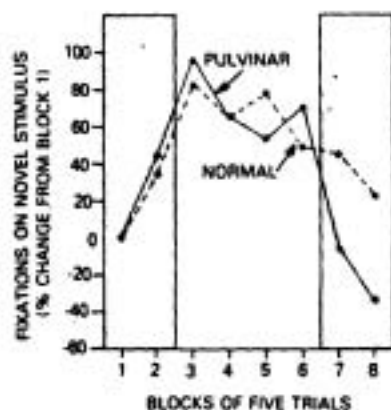


FIG. 3. Visual fixations directed to the novel stimulus by normal monkeys and by monkeys with pulvinar lesions. Trial blocks 1, 2, 7, and 8 are the control trials in which all figures within the array, including the novel stimulus, appeared white on a black background; trial blocks 3 through 6 are the trials in which the novel stimulus was colored red. The data in this and all subsequent figures are the combined results from the 2 days of testing.

added. On the first five novelty trials, trial block 3, fixations on the novel stimulus increased to an equal extent for both groups ($U = 7$, $P = 0.886$). Habituation to this novel stimulus occurred at varying rates for individual animals, but was clearly evident in all monkeys by trial block 6. There was no significant difference in the rate of habituation from trial block 3 to trial block 6 between the normal and operated groups ($U = 5$, $P = 0.486$). Although monkeys with pulvinar lesions appeared to ignore the novel stimulus when it was no longer colored red, this effect was not significant on trial block 7 ($U = 4$, $P = 0.342$) or trial block 8 ($U = 5$, $P = 0.486$).

Visual scanning

A comparison of the distribution of visual fixations directed on and off the stimulus array for monkeys in Groups P and N indicated that pulvinar lesions produced a restricted pattern of visual scanning. As shown in Fig. 4, normal monkeys fixated the stimuli approximately 60% of the time throughout testing; that is, almost 40% of their fixations were directed off the stimulus display. This was true even on trial blocks 2 and 3 when the novel stimulus was present. By contrast, monkeys with pulvinar lesions consistently maintained attention to the stimuli; fewer than 15% of their fixations were directed off the display, a significant difference from normal monkeys ($U = 1$, $P = 0.058$). Although there was a trend for the operated monkeys to make fewer total fixations than normal monkeys, this effect was not significant ($U = 2$, $P = 0.114$).

Duration of visual fixations

A comparison of the mean duration of visual fixations of monkeys in Group P with those in Group N showed that, throughout testing, the fixations of the operated animals were abnormally prolonged. Data in Fig. 5 indicate that, for normal monkeys, the duration of visual fixations consistently averaged between 210 and 270 msec, whether the animals were fixating the novel stimulus or fixating one of the other 15 figures in the array. Thus,

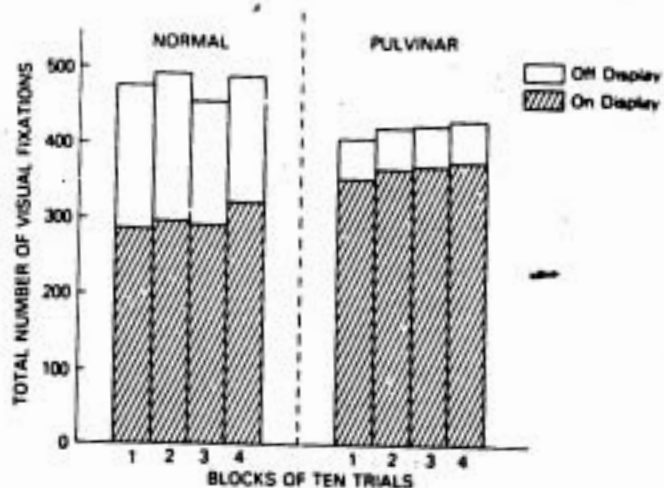


FIG. 4. Distribution of visual fixations directed to the stimuli within the array (on display) and directed off the array (off display) for normal monkeys and for monkeys with pulvinar lesions. Each fixation is defined as one 200-msec video tape frame.

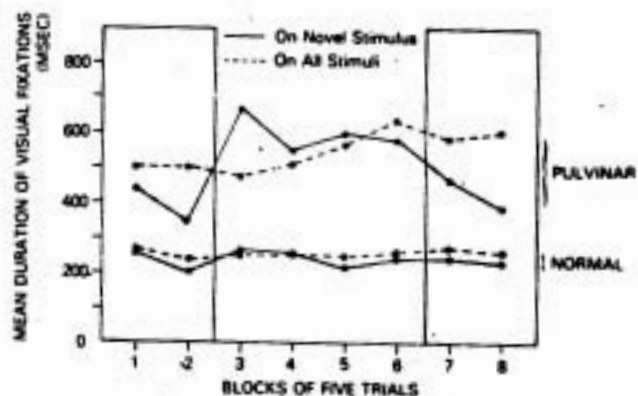


FIG. 5. Mean duration of visual fixations (msec) over the course of testing for normal monkeys and for monkeys with pulvinar lesions. The data are averaged separately for those fixations directed toward the novel stimulus and for those fixations directed toward all the other 15 figures in the stimulus array.

despite the fact that normal monkeys oriented to the novel stimulus (see Fig. 3), the duration of their fixations on it was unchanged. Monkeys with pulvinar lesions differed from normal monkeys in two respects. First, their fixations were abnormally prolonged in general: when viewing one of the 15 control stimuli in the array, the fixations of monkeys with pulvinar lesions averaged approximately 300 msec longer than those of normal monkeys ($U = 0$, $P = 0.028$). Second, orientation toward the novel stimulus was accompanied by a significant increase in the duration of fixations on that stimulus for monkeys with pulvinar lesions ($t = 7.58$, $d.f. = 3$, $P < 0.01$).

DISCUSSION

The results of the present study have shown that, although monkeys with pulvinar lesions did not differ from normal monkeys in either visual orientation or habituation to a novel stimulus, damage to the pulvinar did influence visual behavior. Unlike normal monkeys, monkeys with pulvinar lesions appeared visually captured by the stimulus array, showing few saccades to points outside its boundaries. Moreover, these monkeys demonstrated abnormally prolonged fixations, an effect which was enhanced by the novelty or salience of the visual stimulus. These results extend our prior findings by showing that eye-movement abnormalities produced by pulvinar damage occur not only during discrimination learning, but also during spontaneous scanning of visual stimuli.

What is the nature of the impairment underlying these eye-movement abnormalities? The data suggest that the deficits are attributable, at least in part, to a disorder in the processing of visual information. Visual capture has previously been reported in human infants [45] and retardates [46, 47]. In these instances, it has been interpreted as an indication of limited processing capacity. Prolonged fixations by monkeys with pulvinar lesions may reflect an attempt to compensate for such a processing impairment. This hypothesis would explain the finding that monkeys with pulvinar lesions fail visual discrimination problems only when the stimuli are flashed very briefly [48], a situation which would greatly disrupt discrimination learning in animals who require prolonged periods of observation to adequately process visual information.

If this hypothesis is correct, the duration of fixations in monkeys with pulvinar lesions should be a function of the processing demands placed upon the animal, either by the nature of the stimulus fixated or by the complexity of the test situation. The combined results from our two studies show that this is apparently the case. First, when scanning the stimulus array, monkeys with pulvinar lesions fixated the novel stimulus for longer periods than they fixated the other stimuli. Second, their fixations averaged 300 msec longer than normal when the animals spontaneously viewed stimuli, but averaged nearly 500 msec longer than normal when they were required to discriminate between stimuli.

While these data suggest that pulvinar damage produces a disorder in visual processing, a second hypothesis deserves consideration; the eye-movement abnormalities observed after ablation of the pulvinar may be due to alterations in oculomotor function. However, the results of neurological tests indicated that visual pursuit, horizontal nystagmus, convergence, vertical and horizontal saccades, and pupillary reflexes were normal in the monkeys with pulvinar lesions. Although quantitative measurements were not made, their eye-movement velocities appeared normal as well. These findings attest to the basic integrity of the oculomotor system in monkeys with pulvinar lesions, but they do not demonstrate that all aspects of their oculomotor capabilities are normal. For example, they may have difficulty initiating visually-guided eye movements. Their prolonged fixations would then reflect an increased latency to initiate successive saccades. Increases in saccadic latency have been reported in primates following ablation of the superior colliculus [30-33], a structure which projects to the pulvinar [21, 23-26].* However, as discussed in our earlier report, monkeys

*The effects produced by inadvertent damage to the superior colliculus were considered at length in our prior report [39]. Briefly, although the lesions in all four monkeys did encroach on the brachium of the colliculus, the monkeys who demonstrated the most prolonged fixations (P-G17 and P-G19) sustained the most extensive damage, not to the brachium, but rather to the caudal portion of the pulvinar. Thus, while damage to the brachium may contribute to the effects produced by pulvinar lesions, such damage cannot explain them.

with pulvinar lesions are capable of moving their eyes rapidly, although they do not typically do so. Moreover, the visual capture observed in these monkeys is not easily explained by an impairment in the ability to initiate visually-guided eye movements. Nonetheless, rigorous formalized testing of their eye movements both in the light and in the dark will be necessary to determine whether monkeys with pulvinar lesions initiate eye movements normally.

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Résumé :

On a enregistré sur vidéo les mouvements oculaires de singes normaux et de singes avec lésions du pulvinar alors que leur regard balayait spontanément un stimulus complexe. Pendant la session d'examen, une couleur était ajoutée à un des stimulus de la présentation. Bien que les singes avec lésions du pulvinar n'étaient troublés ni dans leur orientation visuelle ni dans l'habituation à ce nouveau stimulus, leurs mouvements oculaires devenaient anormaux de 2 façons : 1° ils apparaissaient capturés optiquement par les stimulus et peu de saccades s'exécutaient en dehors du dispositif; 2° leurs fixations étaient anormalement prolongées. Ces anomalies des mouvements oculaires apparaissent associées à un désordre du traitement visuel plutôt qu'à un trouble du contrôle oculomoteur.

Deutschsprachige Zusammenfassung:

Die Blickbewegungen von normalen Affen und von Affen mit Pulvina-Läsionen wurden auf Video-Bändern registriert, während die Tiere spontan eine komplexe Stimulusanordnung absuchten. Während der Testsitzungen wurde einem Stimulus die Anordnung Farbe beigelegt. Obwohl die Affen mit Pulvina-Läsion weder in ihrer visuellen Orientierung noch in ihrer Gewöhnung an diesen neuen Stimulus eingeschränkt waren, waren die Blickbewegungen in zweierlei Weise abnorm. Zum einen schienen sie durch die Stimuli visuell gefangen, indem sie nur wenige Sakkaden von der Anordnung weg machten. Zum anderen waren ihre Fixationen abnorm verlängert. Diese Abnormalitäten der Blickbewegung schienen eher mit einer Störung in der visuellen Verarbeitung verbunden zu sein als mit einer Einschränkung der oculomotorischen Kontrolle.