THE EFFECTS OF BILATERAL FRONTAL EYE-FIELD, POSTERIOR PARIETAL OR SUPERIOR COLLICULAR LESIONS ON VISUAL SEARCH IN THE RHESUS MONKEY

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SUMMARY

Superior collicular, frontal eye-field and posterior parietal lesions increased the time taken to find a circular target among other geometrical shapes. The collicular monkeys were considerably more impaired than the other groups, suggesting that the superior colliculus is the main neural structure underlying this highly practised visual search task.

Failure to respond in the 5 sec allowed on each trial increased for all groups, and the collicular and frontal groups showed a small increase in false positive errors.

None of the groups increased search time for a near-threshold target on a homogeneous background.

Analysis of the latencies of individual trials suggests that scanpaths over the display were still systematic after the lesions. This suggests that the search was being slowed down either by the need to make more correction saccades to give accurate fixations of the stimuli being discriminated, or by an increase in latencies specifically for those saccades that shift the gaze between stimuli.

INTRODUCTION

Animals with foveas use eye movements to select the visual information contributing to their perceptions. Eye movements are therefore a central part of the visual processing system, and it is not surprising that stimulation and recording experiments have found many areas in the primate's visual system concerned with them. Ferrier, for example, describes oculomotor responses on stimulating the frontal eye-fields, posterior parietal cortex and the superior colliculus, and all these areas have since been shown to contain both neurons responding to eye movements and visual neurons.
What is surprising is that lesions in these areas do not cause marked oculomotor disorders. Unilateral lesions produce an ipsilateral conjugate deviation, certainly after frontal eye-field lesions\textsuperscript{11} and probably after deep collicular lesions\textsuperscript{10} and slight abnormalities in fixation\textsuperscript{14,16,29}. But bilateral lesions appear to produce only a reluctance to shift the eyes from the primary position\textsuperscript{1,11,14,29}. After testing monkeys with frontal eye-field, posterior parietal or collicular lesions on a battery of oculomotor tests, Pasik and Pasik\textsuperscript{20} conclude that there were no significant impairments. Only hemi-decortication produced lasting deficits. This implies considerable redundancy between oculomotor regions, but it may only be for relatively simple functions, like optokinetic nystagmus\textsuperscript{20} or fixation of discrete and isolated stimuli\textsuperscript{16,29}, and that these areas are specialized for more complex tasks, such as organizing scanpaths to sample the visual world in a meaningful way.

The present experiments investigate the effects of frontal, parietal or collicular lesions on monkeys' performance of visual search tasks, where they have to scan a visual display to find a target stimulus.

**METHOD**

**Subjects and surgery**

Eleven, experimentally naive, immature, male rhesus monkeys (Macaca mulatta) received 150 g of Modified Laboratory Animal Diet 41B (Oxo) daily. Inter-spersed with the tests described here was a series of brightness discrimination threshold measurements\textsuperscript{12} using the same apparatus. Bilateral lesions were made as follows: *frontal eye-field* (FEF) (n = 3): cortex within the angle of arcuate sulcus, the area giving eye movements on electrical stimulation\textsuperscript{22}; *posterior parietal* (P) (n = 3): inferior parietal lobule and posterior part of ventral bank of superior temporal sulcus; *superior colliculus* (SC) (n = 2); *control* (C) (n = 3): two unoperated, the third (C3) underwent the same surgery as SC\textsubscript{2}, except that the electrode placements were 5 mm higher and no current was passed. Cortical lesions were made by subpial suction using a fine gauge sucker. Collicular lesions were electrolytic and current parameters and stereotaxic coordinates are given in an earlier paper\textsuperscript{12}.

**Apparatus**

This is described in detail elsewhere\textsuperscript{12}. Pressing an observing response bar on the stimulus-response panel caused the search display to be back projected onto a panel 30 cm wide $\times$ 20 cm high. The display stayed on for 5 sec or until the monkey pressed the panel. If the half of the panel containing the target was pressed, a 190 mg banana flavoured pellet (CIBA Pharmaceutical) was delivered to a well beside it, and a light over the well came on for 3 sec. If the other half of the panel was pressed or no response was made, there was 5 sec darkness. Three hundred trials were given daily and the target appeared on the left or right half of the panel in a random sequence except that no more than three consecutive trials could occur with the same half positive.

The target was a circular patch of light appearing randomly in one of 40 evenly
spaced positions with the constraint that each position occurred twice every 80 trials. Its illumination could be reduced with neutral density filters and it could appear with up to 39 irrelevant stimuli occurring with equal probability in any of the 40 target positions not occupied by the target and arranged so that there were equal numbers of stimuli on the two halves of the panel. The irrelevant stimuli were drawn at random from 7 geometrical shapes: diamond, triangle, square, cross, star, hexagon and asterisk.

The response accuracy and latency (interval between pressing observing response bar and stimulus panel) were recorded. The latency was collected as a frequency distribution using one-third sec bins. To reduce distortion of the mean by trials on which a correct response was made by chance, the frequency distribution for incorrect trials was subtracted from the distribution for correct trials before the mean for correct trials was calculated.

**Experimental design**

Three conditions of visual search were used. *Near-threshold target*: target of diameter 0.7 cm and luminance 1.5 cd m$^{-2}$ against a background of 1.1 cd m$^{-2}$. This was approximately half a log unit above the monkeys' threshold (75% correct)$^{12}$. The monkeys were pretrained to a criterion of 3 days (900 trials) at better than 90% correct. Experimental data were collected from a further 900 trials immediately after reaching criterion and again 2 weeks postoperative. *Hidden target I*: target of diameter 0.8 cm and luminance 343 cd m$^{-2}$ against a background of 1.1 cd m$^{-2}$. There were 6 conditions with 0, 1, 3, 5, 7 or 9 irrelevant stimuli, and they were trained to a criterion of one day (300 trials) at better than 90% correct on each condition before moving on to the next. Data were then collected from 600 trials in each condition, in blocks of 100 trials. The blocks occurred in random order except that each condition was followed by every other condition once. Three blocks a day were given, taking 12 days to complete the total sequence of 3600 trials. This was given immediately after the near threshold condition, both pre- and postoperatively. *Hidden target II*: the stimulus array was as before except that there were 39 irrelevant stimuli. One day's practice was given and then data were collected for the 300 trials of the second day's testing. The luminance of the stimuli was then reduced in daily steps and the monkey was titrated to the 75% correct level until he failed twice. This condition was tested only once, 8 or more weeks postoperative.

**Histology**

The monkeys were anaesthetized and perfused through the heart with 0.9% saline followed by 10% formol-saline. Brains were cut coronally in the stereotaxic vertical plane, removed and left in 30% sucrose formalin until they sank. Frozen sections were cut at 50 μm and every tenth section stained with cresyl violet.

Reconstructions of the lesions are given in Fig. 1. There were some incursions into white matter, particularly with the parietal lesions, but these were not consistent and it is improbable that they could account for the effects described. The two collicular lesions were neither complete nor limited to superior colliculus. SCI spared caudal
Fig. 1. a: reconstructions of the cortical lesions. b: sections, cut in the stereotaxic vertical, through the collicular lesions. Sections in b were drawn at 500 μm intervals and all sections that showed tissue damage are included in the figure.
superior colliculus but spread rostrally into the pretectal region, while SC2 spared rostral superior colliculus but spread caudally, damaging both the inferior colliculus and, to a small extent, the cerebellum. So, apart from slight incursions into central grey, the area common to both lesions was entirely within the superior colliculus.

RESULTS

Visual search with near-threshold target

There were no significant differences between the groups on the three measures of pre- to postoperative change taken: errors, $F = 1.08, P > 0.05$ (Fig. 2); latency, $F = 1.82, P > 0.05$ (Fig. 3); no responses, $F = 0.63, P > 0.05$ (Fig. 4).

Looking at individual animals, there were 2 striking effects. The percentage of
Fig. 2. Pre- to postoperative change in response errors (expressed as a percentage of total responses) for visual search with a near-threshold target. The cross-hatched bars are for individual animals and the open bars are group means. The numbers at the top of each section are the mean performance of that group, preoperative on the left and postoperative on the right.

Fig. 3. Pre- to postoperative change in the latency of correct responses for visual search with a near-threshold target. For explanation, see Fig. 2.
Fig. 4. Pre- to postoperative change in response errors (expressed as a percentage of total responses) for visual search with varying numbers of irrelevant stimuli.

Fig. 5. Pre- to postoperative change in the percentage of no responses for visual search with a near threshold target. For explanation, see Fig. 2.
trials on which FEF1 did not respond increased from 2 to 38. There was a double dissociation between the two collicular monkeys and their error and latency scores: SC1's errors increased from 2 to 44% and SC2's latency increased from 1230 to 1990 msec.

**Visual search with hidden target I**

Change in percentage errors is shown in Fig. 5. The difference between the groups was significant ($F = 5.94, P < 0.01$) and, calculating $t$ using the estimate of variance obtained from the remainder of this analysis of variance, both the collicular group ($t = 4.00, P < 0.001$, one-tailed) and the frontal group ($t = 1.82, P < 0.05$, one-tailed) showed a significantly larger increase in errors than the control group. The parietal group was not different from the controls ($t = 0.67, P > 0.05$, one-tailed).

Change in latency is shown in Fig. 6. The difference between the groups was significant ($F = 10.46, P < 0.001$), and the collicular ($t = 5.58, P < 0.001$, one-tailed), frontal ($t = 2.42, P < 0.01$, one-tailed) and parietal ($t = 2.03, P < 0.05$, one-tailed) groups showed a significantly larger increase than the control group. There was no difference between the frontal and parietal groups ($t = 0.39, P > 0.25$).

![Fig. 6. Pre- to postoperative change in the latency of correct responses for visual search with varying numbers of irrelevant stimuli.](image-url)
Fig. 7. Pre- to postoperative change in the percentage of no responses for visual search with varying numbers of irrelevant stimuli.

Fig. 8. Pre- and postoperative percentage correct and latency scores of the collicular and control monkeys for visual search with varying numbers of irrelevant stimuli.
two-tailed) but the collicular group showed a significantly larger increase than both the frontal ($t = 3.42, P < 0.01$, two-tailed) and parietal ($t = 3.76, P < 0.001$, two-tailed) groups.

Change in percentage of no responses is shown in Fig. 7. The difference between the groups was significant ($F = 2.86, P < 0.05$), and the collicular ($t = 2.91, P < 0.01$, one-tailed), frontal ($t = 3.06, P < 0.01$, one-tailed) and parietal ($t = 3.86, P < 0.001$, one-tailed) groups showed a significantly larger increase than the control group.

Looking at individual animals, the only striking qualitative differences were between the collicular monkeys (Fig. 8). As in the near threshold target condition, only SC1 showed a large decrease in percentage correct. They also showed opposite directions of interaction between the latency change and the number of irrelevant stimuli, but it is possible that SC1's negative interaction was caused by his tendency to make errors. (In the extreme case of a monkey who was unable to discriminate the relevant and irrelevant stimuli and therefore always responded to the first stimulus he saw, the more stimuli there were the shorter his latency would be).

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**Fig. 9.** The effect on visual search latency of dimming the display in the condition with 39 irrelevant stimuli. (The latency was the mean of the first 300 trials performed by each monkey at 75% correct or better for each level of display brightness.)
Visual search with hidden target II

Latency data for this condition are summarized in Fig. 9. This confirms the previous deficit and suggests a learnt improvement in the performance of the frontal and parietal groups. However, two-way analyses of variance comparing each experimental group with the control group, over the range of brightnesses for which all animals in the groups being compared met the 75% criterion (see Fig. 9), showed no significant interaction between group differences and brightness. The only significant overall intergroup difference was between the collicular and control groups ($F = 17.26, P < 0.001$).

Individual trial analysis

Without eye movement recording it is not possible to determine directly whether these visual search deficits were paralleled by changes in scanpaths. It is possible to say something about the consistency of the scanpaths over a series of trials by looking at the relationship between target position and the nature and latency of the response.

All monkeys appeared to scan the display normally, except FEF1 searching for a near-threshold target. His strong tendency not to respond within 5 sec was due to a failure to scan the edges of the display (Fig. 10). There is no way of distinguishing between a failure to see due to failure to fixate and a failure to fixate due to failure to see. But a similar neglect was found previously using stimuli shorter than the latency of a saccade so that seeing was not dependent on eye movements\textsuperscript{13}. This suggests that for FEF1 a failure to see the peripheral display resulted in a failure to scan it.

![Fig. 10. Individual trial analysis of the performance of monkey FEF1 on the visual search with a near-threshold target. The circles show the position of the target on each of 100 trials. Filled circles signify a failure to respond. Crosses signify an incorrect response. Numbers indicate the latency, in tenths of a second, of a correct response.](image-url)
Fig. 11. Individual trial analysis of the performance of monkey SC2 on the visual search with (A) near-threshold target, (B) 39 irrelevant stimuli. For explanation of symbols see Fig. 10.

Fig. 10. also shows that FEF1, the slowest of the frontal group, had a strong tendency to scan systematically, starting at the centre of the right panel and ending at the bottom of the left panel or the bottom left corner of the right panel. SC2, the most impaired of the collicular monkeys, also showed a systematic scanpath. Fig. 11 shows that with both the near-threshold target and 39 irrelevant stimuli he usually began in the upper centre of the right panel and ended at the top of the left panel.

This pattern in the individual trial data was quantified by dividing each panel
TABLE I

The means and standard deviations of the segment latencies (in msec) for those monkeys and conditions for which an individual trial analysis was made

<table>
<thead>
<tr>
<th>Monkey</th>
<th>Experiment</th>
<th>Near-threshold target</th>
<th>Postoperative</th>
<th>Hidden target</th>
<th>Log reduction factor</th>
</tr>
</thead>
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<td></td>
<td></td>
<td>Preoperative</td>
<td>Postoperative</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>S.D.</td>
<td>Mean</td>
<td>S.D.</td>
</tr>
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<td>1960</td>
<td>470</td>
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<tr>
<td>FEF2</td>
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<td>960</td>
<td>250</td>
<td>1400</td>
<td>260</td>
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<td>800</td>
<td>190</td>
<td>1126</td>
<td>180</td>
</tr>
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<td>253</td>
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<td>860</td>
<td>220</td>
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</table>

into 4 equal horizontal segments, giving a total of 8 segments, and averaging the response latency for all the targets within each segment. (This showed, for example, that in Fig. 11 the segments having the fastest and the slowest latency remained the same in the two conditions.) If a scanpath varied randomly from trial to trial, beginning and ending at different points on each trial, the mean latency would be the same for each segment and the standard deviation of these means would be zero. The more systematic the scanpath was, the larger the standard deviation would be. So a lesion that disrupted the scanpath would reduce the standard deviation. The means and standard deviations of the segment latencies for the conditions analyzed are shown in Table I. (This analysis was not done for the conditions with 1–9 irrelevant stimuli since the stimulus configuration itself varied spatially from trial to trial in a random way.) Standard deviations are clearly not lower for operated animals and so the tentative conclusion must be that, although eye movements of operated animals may have been slower, their scanpaths were not disrupted.

DISCUSSION

The experimental groups took longer to search with varying numbers of irrelevant stimuli (hidden target I), but with a near-threshold target there were no significant differences, although two parietal and one collicular monkey showed a considerably larger increase than any control. The difference between these conditions cannot be attributed to increased difficulty, since in terms of search time the near-threshold condition was more difficult, nor to recovery of function, since the near-threshold condition was tested first. It might be due to an increase in the time taken to make a form discrimination, although it seems unlikely that this would not also impair the
near-threshold search task. Or, more likely, it might be that the presence of several stimuli requires the eye to saccade accurately between them so that a decrease in saccadic accuracy, of the kind reported after collicular lesions, would necessitate more correction saccades and result in a slower search. The near-threshold search would not be affected since here the eyes were scanning across a homogeneous screen. Another possibility is that the lesions increased the latency of saccades, also found after collicular lesions, but only of those shifting the gaze between stimuli. (An increase in the latency of all saccades would affect both conditions equally.)

Both collicular monkeys showed an increase in search time in the hidden target condition but only SCI showed an increase in incorrect panel presses (Fig. 8). The absence of a discrimination deficit in SC2 could be due to sparing of anterior colliculus which receives its input from foveal retina and, if the colliculus is involved in form discriminations, would therefore be crucial. Or the critical area might be the pretectum, damaged in SCI but spared in SC2. In the rat, this is important for brightness discrimination. One previous study has shown pattern discrimination deficits after pretectal lesions in monkeys, but they have not been found after collicular lesions, except in the tree shrew and the cat. But lesions in the monkey have always been incomplete and the problem needs further investigation.

The frontal eye-field group also showed an increase in incorrect panel presses with varying numbers of irrelevant stimuli. But the increase was small and no animal fell below 90% correct. Discrimination deficits have not previously been found after frontal eye-field lesions, so it is likely that this small effect was due to visual search difficulties rather than vice versa. The parietal group showed no increase in incorrect panel presses.

All experimental groups showed a small increase in the trials with varying numbers of irrelevant stimuli on which they pressed neither panel. The simplest explanation is that an increase in search time meant more trials on which the stimulus was not found within the 5-sec limit. FEFI also showed a dramatic increase in no-response trials in the near-threshold condition, similar to the neglect after a bilateral frontal eye-field lesion of an earlier study.

The consistent scanpaths found in the individual trial analysis is similar to findings in man. The failure to find a disruption of scanpath does not mean that none of the structures lesioned is involved in the use of a systematic scanpath to select features of a pattern in a fixed sequence — a central process in pattern recognition, for eye movements between stimuli may be different from movements within patterns. Some of the experimental groups might show disrupted scanpaths while looking at complex pictures. Certainly Tyler, in a study of patients with large frontal lesions, found scanning deficits with complex pictures but not with simple geometrical shapes.

There were large individual differences between animals both pre- and postoperative. The only interesting relationship was for frontal eye-field animals where the rank order for trials to criterion in training was the same as for the postoperative latency increase. So, the more practice a monkey had preoperatively, the smaller the effect of the frontal eye-field lesion. In humans, visual search is different in naive and
highly practised subjects, and the hypothesis that the frontal eye-fields are involved in learning a new search strategy but not in a highly practised search of the kind used here will be tested in a later experiment.

The deficits found make it reasonable to conclude that the superior colliculus, the frontal eye-fields and the posterior parietal region are all involved in visual search. But the larger increase in search time after lesions of the superior colliculus suggests that this is the most important neural mechanism underlying this kind of highly practised visual search.

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REFERENCES


