

## **The effects of bilateral frontal eye-field lesions on the learning of a visual search task by rhesus monkeys**

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One of the main functions of the oculomotor system is to explore the visual environment in order to locate specific targets. There are situations, for example a predator lying in wait for prey, in which the same scene is explored repeatedly and a particular search strategy develops, enabling the scanpaths followed by the eyes to become systematized and repetitive<sup>14</sup>. Investigations of visual search in man suggest that a practised subject performs differently from a naive subject. For example, the more targets a naive subject is looking for, the longer he takes to scan the display, while a highly practised subject can search for several targets as quickly as for one<sup>13</sup>. This led to the suggestion<sup>9</sup> that different neural mechanisms might be involved in learning a new visual search and in performing a highly practised search. It might be that mechanisms are used in the initial structuring of an efficient scanpath that are not required once the search has become practised.

A previous study of visual search in monkeys<sup>9</sup> found that scanpaths for highly practised monkeys were indeed consistent from trial to trial. The study also showed that frontal eye-field lesions produced an increase in the time taken to perform this highly practised visual search. The monkeys were trained preoperatively to a criterion based on accuracy of target discrimination rather than speed of performance, so there were considerable variations in the amount of practice they had had. For the 3 monkeys with frontal eye-field lesions tested, the less practice they had had preoperatively the larger was the effect of the lesion. Further, the only monkey whose scanpath was qualitatively disrupted was the monkey who had had by far the least practice preoperatively (44 days training, compared with 131 days and 140 days for the other two monkeys). This suggested the exciting possibility that the frontal eye-fields are important in the early, learning stages of a visual search but only peripherally involved in the mediation of a highly practised visual search, for which the superior colliculus seemed to be the more important structure<sup>9</sup>.

The present experiment tested this hypothesis by training monkeys postoperatively to search for a circular target appearing in random positions among 39 other geometrical shapes. Monkeys with frontal eye-field lesions learnt to perform the task accurately in the same number of trials as normal controls but they were consistently

slower in finding the target. Although all monkeys learned to search faster over 12 days of testing, the frontal eye-field deficit remained constant throughout. The hypothesis that the frontal eye-fields are concerned primarily with organizing new visual search strategies is therefore rejected. Instead, an explanation of the deficit in terms of an impairment in spatial attention is suggested.

The apparatus has been described in detail in an earlier paper<sup>8</sup>. The monkey had free access during a test session to a vertical and fully automatic stimulus-response panel. Pressing an observing response bar caused the search array to be back-projected onto a 'pearlite' panel 30 cm wide by 20 cm high. The projector shutter stayed open for 5 sec or until the monkey pressed the panel. If the half of the panel containing the target stimulus (see below) was pressed, a 190 mg banana-flavoured food pellet (CIBA Pharmaceutical) was delivered to a food-cup beside it and a small light over the food-cup was switched on for 3 sec. If the other half of the panel was pressed or if no response was made, there was a 5 sec period of darkness in the testing chamber. Each monkey was given 250 trials daily and the target stimulus appeared on the left or right half of the panel in a sequence that was random except for the constraint that no more than 3 consecutive trials could occur with the same panel positive.

The target stimulus was a circular patch of light with a diameter of 0.8 cm and a luminance of 343 cd/sq.m against a background of 1.1 cd/sq.m. It appeared randomly in one of 40 positions evenly spaced over the response panel, with the constraint that it must occur twice in each position in every 80 trials. It could be made to 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 always equal numbers of stimuli on the two halves of the panel. The irrelevant stimuli had the same luminance as the target and were drawn at random from 7 geometrical shapes: diamond, triangle, square, cross, star, hexagon and asterisk. The response accuracy and latency (the interval between pressing the observing response bar and pressing the stimulus panel) were recorded.

Six immature male rhesus monkeys (*Macaca mulatta*) were used. They were partially food-deprived during testing, receiving about 150 g of Modified Laboratory Animal Diet 41B (Oxo Ltd.) daily. Three monkeys had the cortex within the angle of the arcuate sulcus and on the dorsal bank of the superior arm of the arcuate sulcus removed bilaterally 8–11 weeks before the start of testing (see Fig. 1). Surgery was performed under deep Nembutal anaesthesia using fully sterile techniques, and cortical tissue was removed by subpial suction using a fine gauge sucker. The other 3 monkeys were unoperated controls.

Prior to this experiment, the monkeys had been tested in an apparatus that measured their accuracy of reach<sup>11</sup>. Although the visual display was quite different to the present one, the overall response pattern was similar: the monkey had to press an observing response lever (identical in design and position in the two experiments) to initiate a trial and then had to press whichever of a horizontal row of levels was illuminated. This similarity meant that there was almost immediate transfer to the visual search apparatus, and thus the confounding of the learning of the visual

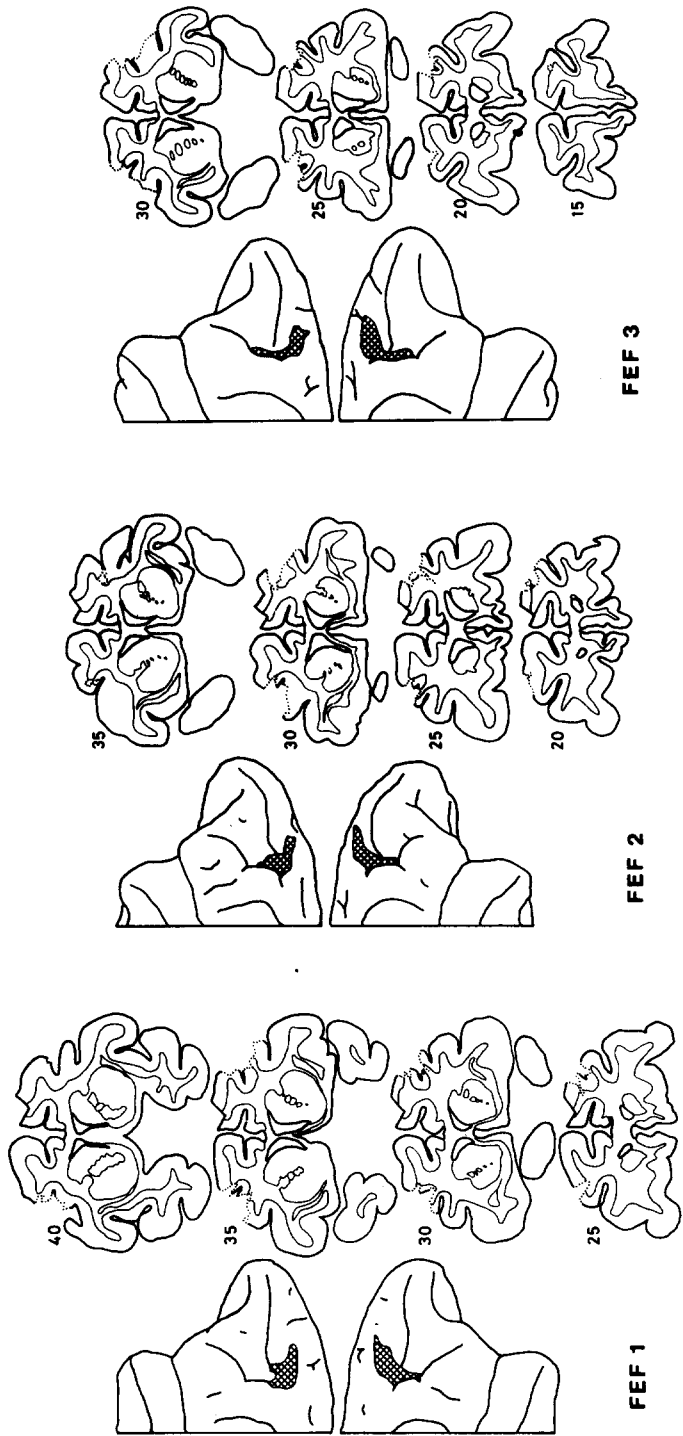


Fig. 1. Reconstructions of lateral views of the lesions (shown cross-hatched) and tracings of sections taken at 2.5 mm intervals through the lesions (shown dotted).

search by the need to learn to operate the apparatus was kept to a minimum.

Monkeys were introduced to the final search condition with 39 irrelevant stimuli via two simpler conditions:

*Target alone:* the target appeared without irrelevant stimuli. Before the first day's block of 250 trials was run, the monkey was given 10 trials in which the experimenter shaped his responses. (This was the only point in the experiment that shaping was done and in most cases even this proved unnecessary and the monkey simply ran 10 trials for which data were not collected.) They were then tested on this condition to a criterion of 90% correct over one day's testing (225/250 trials correct) and transferred to:

*Target with one irrelevant stimulus:* a single irrelevant stimulus appeared in the opposite half of the response panel to the target stimulus. After reaching a criterion of 90% correct over one day's testing, they were immediately transferred to the final condition:

*Target with 39 irrelevant stimuli:* they were given 250 trials/day on this condition until they had completed 12 days testing at 75% correct or better.

At the end of the experiment, the operated monkeys were anaesthetized with Nembutal and perfused through the heart with 0.9% saline followed by 10% formol-saline. The brains were cut coronally in the stereotaxic vertical plane, then removed, photographed and left in 30% sucrose formalin until they sank. Frozen sections were cut at 50  $\mu\text{m}$  and every tenth section was stained with cresyl violet.

Reconstructions of the lesions are shown in Fig. 1. They were as intended with the exception that in all cases there was some sparing of cortex in the very depths of the arcuate sulcus and there was slight damage to white matter. The banks of sulcus principalis were undamaged.

The mean number of trials taken to reach the criterion of 90% correct on each of the three conditions was: target alone, 290 trials; one irrelevant stimulus, 630 trials; 39 irrelevant stimuli, 790 trials. The difference between the groups was never significant: target alone  $t = 0.0048$ ,  $P > 0.05$ ; one irrelevant stimulus,  $t = 0.0009$ ,  $P > 0.05$ ; 39 irrelevant stimuli,  $t = 0.0002$ ,  $P > 0.05$ . Neither was there a significant difference in the speed with which the two groups found the target when performing at 90% correct or better in the first two conditions: target alone,  $t = 0.00004$ ,  $P > 0.05$ ; one irrelevant stimulus,  $t = 0.00009$ ,  $P > 0.05$ .

The performance of the two groups in learning the condition with 39 irrelevant stimuli is shown in Fig. 2. There was no difference between the groups on the percentage of trials they performed correctly ( $F = 0.72$ ,  $P > 0.05$ ). The group with frontal eye-field lesions was slower in finding the target than the control group ( $F = 10.69$ ,  $P < 0.01$ ). There was also an increase in the speed with which the two groups found the target over the 12 days of testing ( $F = 3.95$ ,  $P < 0.001$ ), presumably reflecting an increase in the efficiency with which they scanned the display. However, and this is the test of the hypothesis under consideration, there was no interaction between this learning effect and the difference between the two groups ( $F = 0.07$ ,  $P > 0.05$ ): monkeys with frontal eye-field lesions increased the efficiency with which they scanned the display at the same rate as the normal monkeys. This, together with the lack of

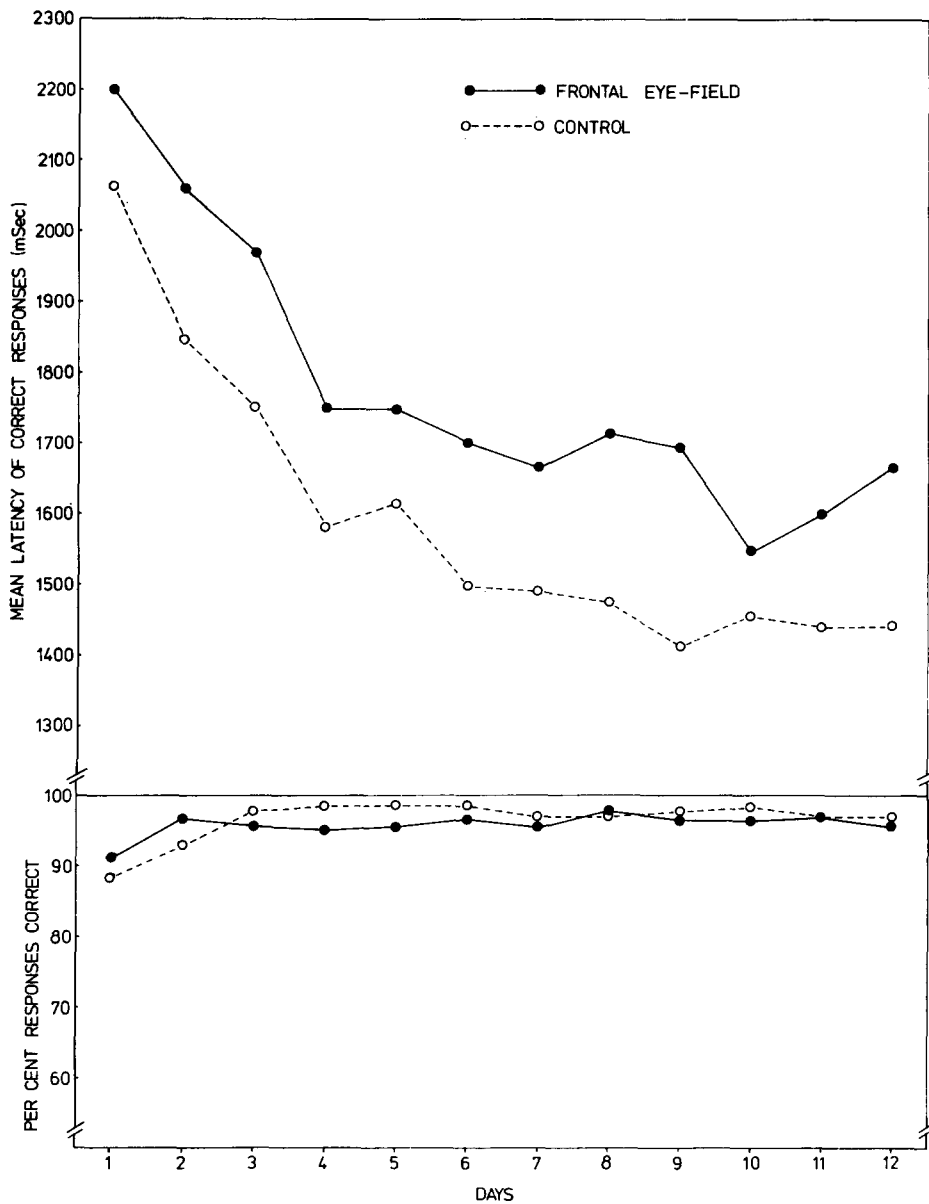


Fig. 2. Mean latencies and percentages correct (250 trials/day) on the condition with 39 irrelevant stimuli.

group differences in the pretraining sessions, means that the hypothesis that the frontal eye-fields are concerned primarily with learning or organizing visual search strategies has to be rejected.

The finding that frontal eye-field lesions produced a decrease in visual search speeds for a postoperatively learnt task confirms and extends the earlier finding of a deficit in a highly practised preoperatively learned task<sup>9</sup>. By the twelfth day of testing

at better than 75% correct, the normal monkeys in this experiment were performing the search in a mean time of 1440 msec, similar to the 1340 msec found with preoperative training, and the frontal eye-field group was 17% slower, compared to 20% slower with preoperative learning. So the size of the deficit was very similar in the two experiments.

The previous study<sup>9</sup>, unlike this one, also produced a small increase in response errors — i.e. there was a small discrimination deficit. A discrimination deficit has also been found by Brody et al.<sup>2</sup>, after much larger lateral frontal lesions, including the frontal eye-fields, when the two stimuli to be discriminated appeared in random positions. The lesions in the earlier visual search study<sup>9</sup> were very similar to those in the present paper except that they extended further down the superior bank of the inferior arm of arcuate. This tissue was deliberately spared in the present study because from recent stimulation experiments<sup>16</sup> it does not seem to be concerned with eye movements. So the discrimination deficit might be due to damage to the inferior arcuate region, an area also included in the lesions in Brody's study.

There are several reasons why search time might be increased after frontal eye-field lesions. An increase in saccade latency or a decrease in saccade accuracy would both increase search time. However, the electrophysiological evidence<sup>1,12</sup> suggests that the frontal eye-fields are not concerned with generating saccades, for the firing of oculomotor units follows rather than precedes the initiation of an eye movement, but rather with monitoring eye movements for some more complex cognitive function. It might be that the frontal eye-fields are concerned with developing a spatial schema of the world and that their destruction causes distortions in perceived spatial relationships between stimuli, making the organization of a visual search difficult. However, a rough analysis of scanpaths of frontal eye-field monkeys in the previous study<sup>9</sup> suggested that they were still scanning the display in as systematic a way as normals. So the most likely explanation of this visual search deficit is not in terms of disorders in oculomotor function or spatial schema, but in terms of spatial attention. The most striking deficit of monkeys with frontal eye-field lesions is a failure to see peripheral stimuli<sup>10</sup>. It was suggested in an earlier paper<sup>8</sup> that this is due to a loss of the mechanism for gating or facilitating visual information in terms of its spatial origins which enables us to attend to a particular region of the visual field and improve discriminability within that region<sup>3,6,18</sup>. In visual search, attending to a region of the visual field is a precursor to foveation (see, for example, the flow diagram for visual search suggested by Engel<sup>4</sup>), so a severe disruption of spatial attention might be expected to result in a search that was still systematic but which was spatially limited to only part of the display. This effect has been reported in human frontal patients<sup>7</sup> and in one of the frontal eye-field monkeys in the previous visual search experiment<sup>9</sup>. A milder deficit in spatial attention might simply slow down attention shifting and result in a visual search that was normal except for a slight reduction in search speed.

A spatial attention deficit of this kind would also cause the impairment in shifting gaze between stimuli reported in cats with frontal eye-field lesions<sup>17</sup> and would, at the least, contribute to the impairments in various tasks with spatial components that have been reported in primates with frontal lesions<sup>2,5,15</sup>.

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- 1 Bizzi, E., Discharge of frontal eye field neurons during saccadic and following eye movements in unanaesthetized monkeys, *Exp. Brain Res.*, 6 (1968) 69–80.
- 2 Brody, B. A., Ungerleider, L. G. and Pribram, K. H., The effects of instability of the visual display on pattern discrimination learning by monkeys: dissociation produced after resections of frontal and inferotemporal cortex, *Neuropsychologia*, 15 (1977) 439–447.
- 3 Engel, F. L., Visual conspicuity, directed attention and retinal locus, *Vision Res.*, 11 (1971) 563–576.
- 4 Engel, F. L., Visual conspicuity, visual search and fixation tendencies of the eye, *Vision Res.*, 17 (1977) 95–108.
- 5 Goldman, P. S. and Rosvold, H. E., Localization of function within the dorsolateral prefrontal cortex of the rhesus monkey, *Exp. Neurol.*, 27 (1970) 291–304.
- 6 Grindley, G. C. and Townsend, V., Voluntary attention in peripheral vision and its effects on acuity and differential thresholds, *Quart. J. exp. Psychol.*, 20 (1968) 1–9.
- 7 Karpov, B. A., Luria, A. R. and Yarbuss, A. L., Disturbances of the structure of active perception in lesions of posterior and anterior regions of the brain, *Neuropsychologia*, 6 (1968) 157–166.
- 8 Latto, R., The effects of bilateral frontal eye-field, posterior parietal or superior collicular lesions on brightness thresholds in the rhesus monkey, *Neuropsychologia*, 15 (1977) 507–516.
- 9 Latto, R., The effects of bilateral frontal eye-field, posterior parietal or superior collicular lesions on visual search in the rhesus monkey, *Brain Research*, 146 (1978) 35–50.
- 10 Latto, R. and Cowey, A., Visual field defects after frontal eye-field lesions in monkeys, *Brain Research*, 30 (1971) 1–24.
- 11 Latto, R. and Marzi, C. A., Neural mechanisms for localizing visual stimuli in the rhesus monkey, *Exp. Brain Res.*, 23, Suppl. (1975) 120.
- 12 Mohler, C. W., Goldberg, M. E. and Wurtz, R. H., Visual receptive fields of frontal eye field neurons, *Brain Research*, 61 (1973) 385–389.
- 13 Neisser, U., *Cognitive Psychology*, Appleton-Century-Crofts, New York, 1967, pp. 66–71.
- 14 Noton, D. and Stark, L. A., Scanpaths in saccadic eye movements while viewing and recognizing patterns, *Vision Res.*, 11 (1971) 929–942.
- 15 Pohl, W., Dissociation of spatial discrimination deficits following frontal and parietal lesions in monkeys, *J. comp. physiol. Psychol.*, 82 (1973) 227–239.
- 16 Robinson, D. A. and Fuchs, A. F., Eye movements evoked by stimulation of frontal eye fields, *J. Neurophysiol.*, 32 (1969) 637–648.
- 17 Schlag-Rey, M. and Lindsley, D. B., Effect of prefrontal lesions on trained anticipatory visual attending in cat, *Physiol. Behav.*, 5 (1970) 1033–1041.
- 18 Van der Heijden, A. H. C. and Eerland, E., The effect of cueing in a visual signal detection task, *Quart. J. exp. Psychol.*, 25 (1973) 496–503.