THE ROLE OF INFERIOR PARIETAL CORTEX AND THE FRONTAL EYE-FIELDS IN VISUOSPATIAL DISCRIMINATIONS IN THE MACAQUE MONKEY

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Macaque monkeys with bilateral lesions of either the frontal eye-fields (Area 8) or the inferior parietal lobule (Area 7a or PG) were compared with unoperated controls on their ability to perform a series of 8 pre-operatively learnt visual discriminations. Simple non-spatial discriminations were not affected, but the frontal group was affected when the stimuli in a shape discrimination varied in position from trial to trial and the parietal group was impaired on the judgement of centre. Both groups were impaired on a spatial landmark test which used luminous stimuli presented in the dark, in positions that varied randomly with respect to the monkey so that only allocentric cues were available. Postoperative trial-by-trial error analysis on the landmark test showed that, whereas spatial discriminability was a factor in determining the performance of the experimental groups, degree of cue–response separation and response perseveration were not. A comparison of the performance of the two groups on all 8 tests suggests that although both are impaired on spatial discriminations, the frontal eye-fields are concerned with spatially organising responses to explore the environment, while the inferior parietal lobule is concerned more directly with the processing of spatial information and the perception of spatial relationships.

INTRODUCTION

A common thread running through the descriptions of visual deficits after lesions to the frontal eye-fields (Area 8) or the inferior parietal lobule (Area 7a or PG) in primates is that tasks showing impairments usually involve spatial manipulations or discriminations. Neither lesion normally impairs non-spatial functions such as pattern discrimination, although unilateral frontal eye-field and possibly inferior parietal lesions can affect visual detection. This contrasts with the primarily non-spatial visual deficits after lesions to the third major area outside visual cortex receiving visual information, the inferotemporal cortex. This double dissociation suggests that the perception of spatial relationships and the perception of objects are handled separately in the brain. (For fuller reviews, see refs. 7,11,15,16,36.)

The exact nature of the spatial functions of the frontal eye-fields and the inferior parietal lobule remains uncertain. In monkeys, lesions to both areas result in impairments in the visual exploration of a display\(^{13,14}\) and, for frontal eye-field lesions at least, in the spatial organisation of a systematic manual exploration of their environment\(^5\). Both lesions also impair spatial discriminations. Pohl\(^{29}\) compared the effects of large dorsolateral frontal lesions, which included most of the frontal eye-fields, both banks of sulcus principalis and much of the lateral convexity dorsal to principalis, with the effects of large posterior parietal lesions, which included the inferior parietal lobule but extended back into prestriate cortex.
(OA) as far as the fundus of lunate sulcus. The frontal lesions, but not the parietal lesions, caused impairments in learning to choose the right-hand one of two identical plaques and in subsequent reversals of this (i.e. a place-reversal task). On the other hand, the parietal lesions, but not the frontal lesions, caused impairments on two landmark tasks. When they had to choose which of two identical plaques was touching a third, distinctive landmark, monkeys with parietal lesions were normal on the initial learning and on the first 3 reversals of this, but on the fourth and subsequent reversals they did show an impairment, failing to improve their performance as quickly as normal monkeys. They were also impaired on the post-operative recall of a task in which they had learnt preoperatively to choose which of two identical plaques was nearer (2" vs 7") the landmark. Pohl concluded that there were two distinct mechanisms for spatial functions. A frontal one, concerned with discriminating position relative to the subject (egocentric position), and a parietal one, concerned with discriminating the relative position of one object with respect to another (allocentric position).

This dissociation of egocentric and allocentric judgements is supported by the clinical comparisons of frontal and parietal lesions made by Semmes et al. 32 and Butters et al. 4, though with the added complication that it seems to relate to the left hemisphere/right hemisphere dissociation as well (see also ref. 30). However, there are a number of difficulties with the interpretation of Pohl's experiments.

(1) There are two distinct reasons for doubting that the deficit in Pohl's landmark task was necessarily due to a deficit in allocentric judgement. First, as Mendoza and Thomas 22 pointed out, the landmark task is different from the place-reversal task in that there is a separation of the cue from the response/reward site in the former but not the latter. They went on to show that increasing the size of the cue–response separation, without changing the spatial discrimination, increased the deficit and they concluded that the impairment was due, not to difficulties in making allocentric judgements, but rather to difficulties in shifting attention, albeit spatial attention, from the reinforcement position to the cue position. (Iwai 12 has also recently argued that the parietal deficit is primarily due to difficulties in coping with cue–response separation and that the inferior parietal lobule is concerned with 'attending selectively to the cue in irrelevant background or visual space'.) Ungerleider and Brody's subsequent demonstration that monkeys with similar large parietal lesions are impaired on simple tangled string problems 35 does not, as they claimed, rule out this alternative explanation, since their task also involved a large spatial separation of the response, the cue and the reinforcement. The second, quite different, reason for doubting the necessity of an allocentric interpretation lies in the particular form of landmark task which Pohl used. Since the response/reinforcement positions were fixed, it was possible for the monkey to solve the task by treating it as a conditional, two-stage, egocentric discrimination: landmark left – go left; landmark right – go right. In this way the monkey could avoid making allocentric judgements at all and Pohl's dissociation reduces to that between two forms of egocentric discrimination. Also, this might be connected, it is puzzling that in several studies, including Pohl's first landmark task, the initial learning of the task has been normal and deficits have only appeared on reversal 29, 35.

(2) The frontal-parietal/egocentric-allocentric double dissociation has not always been confirmed by subsequent experiments. Several have found deficits in landmark 22, 23 or landmark-like tasks after frontal lesions. Both Ungerleider and Brody 35 and Milner et al. 23 suggest that this frontal deficit might be due to response perseveration caused by damage to the inferior convexity of the frontal lobes. Milner et al. do find some evidence in their own experiments of a relative increase in perseverative errors in their frontal group, but Ungerleider and Brody's own experiments do not support the perseverative hypothesis. Other authors have failed to find deficits on the landmark test after parietal lesions 28, 31, but see the next section.

(3) The lesions in Pohl's and most subsequent studies 1, 22, 23, 25, 29, 35 were large and both frontal and parietal lesions included several different
anatomical and functional sub-divisions. The parietal lesions have normally included both the inferior parietal lobule (PG) and dorsal prestriate cortex (OA); areas which, from their anatomy and electrophysiology, we should expect to have very distinct functions (see refs. 6,11,20 for example). Attempts to fractionate the parietal deficit have either failed to find an impairment at all with sub-total lesions28,31, or have found a mass-action effect with the size of the deficit related to the size of the lesion, irrespective of its site within the PG and dorsal OA region. Remarkably, although deficits on the landmark task are often cited as evidence for the spatial function of PG19,21, lesions to PG alone have never been convincingly shown to produce a deficit on the landmark task. (Mishkin et al.24 found that, when grouped together, monkeys with lesions of PG or dorsolateral OA or dorsomedial OA were impaired relative to their preoperative performance, but it is not clear whether their PG group considered alone was impaired, nor was there a normal control group for comparison.) The frontal lesions used in landmark studies have always included at least the frontal eye-fields and the dorsal convexity extending from the ventral bank of sulcus principalis to the mid-line1,22,23,29,35. Again, other evidence suggests that although these two areas both have spatial functions they are rather different in nature, with frontal eye-field lesions producing spatial neglect17 and deficits in organising the exploration of the local environment5,13,14, while sulcus principalis lesions produce impairments on spatial delay tasks3.

The present experiment attempts to resolve some of these problems. It uses a series of behavioural tests to compare the effects of lesions in two clearly identifiable anatomical and functional sub-divisions of parietal and frontal cortex which our previous work has suggested are concerned with the immediate spatial analysis of the visual environment15, the inferior parietal lobule (Area 7a or PG) and the frontal eye-fields (Area 8). The two principal tests used were designed to tackle the questions raised in (1) above. They were a spatial task that minimised cue–response separation (judgement of 'centre'), and a landmark test where the only cues were allocentric (achieved by using luminous stimuli presented in the dark to avoid distracting field dependence effects and in positions that varied randomly with respect to the monkey so that egocentric information was irrelevant to the solution of the problem).

MATERIALS AND METHODS

Subjects, surgery and histology

Nine, immature, male, experimentally naive monkeys were used as subjects, 6 rhesus (Macaca mulatta) and 3 cynomolagus (Macaca fascicularis). Two rhesus and one cynomolagus were allocated to each of 3 groups to give as close a match as possible between the pre-operative learning scores of the groups. (The cynomolagus monkeys were IP3, FEF3 and C3.) Monkeys in the IP group were given bilateral lesions of Area PG37, extending from the fundus of superior temporal sulcus across the inferior parietal lobule to the fundus of intraparietal sulcus, with the ventral boundary defined approximately by a line drawn between the ventral tip of the intraparietal sulcus and the junction of the superior temporal and lunate sulci. Monkeys in the FEF group were given bilateral lesions of Areas FDA and FDF37, the area within the angle of arcuate sulcus, including the anterior banks of both arms of that sulcus and both banks of the posterior portion of principalis. Group C was an unoperated control group.

Surgery was performed under aseptic conditions using intramuscular ketamine hydrochloride to initiate anaesthesia and intravenous sodium thiopentone to maintain it. Lesions were made by sub-pial aspiration through a 20/22 gauge sucker.

At the end of the experiment, the monkeys were given an overdose of Nembutal and perfused through the heart with 0.9% saline followed by 10% formol-saline. The brains were removed and infiltrated with a mixture of 10% formalin and 30% sucrose. They were then photographed and cut while frozen into 50-μm coronal sections. Every tenth section was saved and stained with Cresyl violet.
Reconstructions of the lesions are shown in Fig. 1. Generally the lesions were smaller than intended, with sparing of the depths of the sulci, particularly the intraparietal sulcus, and of the ventral part of FDI. The only lesions that extended outside the intended areas were on the left side of IP1, where there was some damage to the dorsal part of the posterior bank of superior temporal sulcus (see section 30), and the left side of FEF3, where there was damage to the dorsal bank of the superior arm of arcuate sulcus (see sections 19 and 24). The variations in extent of the lesions did not seem to correlate with any behavioural differences between the monkeys.

Apparatus and procedure
All testing was carried out in a Wisconsin General Test Apparatus in a darkened room with a background of masking white noise. A horizontal matte grey testing board, 15 cm higher than the floor of the monkey's transport cage, was used throughout the experiment. It contained a matrix of 36 food-wells, shown diagramatically in Fig. 2. The front edge of the testing board was about a centimetre from the bars of the transport cage so that the whole board was well within the monkey's reach. All the plaques used in discrimination testing were made from 3 mm thick perspex. They were either circular (5.6 cm diameter) or square (5 cm side) and they could be black, white or luminous (white perspex coated with luminous paint). The compartment containing the testing board was illuminated with an overhead 30-W filament strip light. The monkey's compartment was illuminated with an overhead 25-W bulb. A one-way viewing screen between the
Fig. 1. Lateral views and coronal sections for the lesions in the inferior parietal (IP) and frontal eye-field (FEF) groups. Coronal sections were drawn every 2.5 mm through the lesions. The number beside each section refers to its position in the sequence of stained sections (see text).

experimenter and the testing board enabled the monkey to be observed during each trial and an opaque screen was lowered between the testing board and the monkey except for the duration of the trial.

They were tested for 40 trials a day using peanuts or raisins as a reward. Each monkey was trained to a criterion of 90% correct on 100 consecutive trials on the following series of discriminations both pre-operatively and again post-operatively, starting testing 3 weeks after surgery:

(i) Black$^+$ vs White$^-$ – Fixed position. Two square stimulus plaques, one black and one white, covered food-wells B3 and B7 (Fig. 2) in a pseudorandom alternation and with the food-well under the black plaque always baited.

(ii) Left$^+$ vs Right$^-$ – Fixed position. Two square white plaques were placed over food-wells
Fig. 2. Plan view of the testing board with 36 food-wells, which was used in all the tests described in the text. The stimulus plaques are laid out for Discrimination (iv), Square + vs Circle - – Fixed position.

B3 and B7 (Fig. 2) with the food-well under the lefthand plaque (B3) always baited.

(iii) Centre + vs Left -, Right - – Fixed position. Three square white plaques were placed in a row in front of the monkey, covering food-wells B4, B5 and B6 (Fig. 2), with the food-well under the central plaque (B5) always baited.

(iv) Square + vs Circle - – Fixed position. One circular and one square white plaque covered food-wells B3 and B7 (Fig. 2) in a pseudorandom alternation, with the food-well under the square plaque always baited.

(v) Square + vs Circle - – Luminous stimuli – Fixed position. As Discrimination (iv), except that the lights in both compartments of the Wisconsin Box were turned out before the door between the monkey and the testing board was raised and the plaques were luminous. Both the monkey and the experimenter were therefore in complete darkness during each trial, with the only visible objects being the two plaques.

(vi) Square + vs Circle - – Luminous stimuli – Variable position. As Discrimination (v), except that the two plaques appeared, in a pseudorandom sequence, over any of the food-wells in Rows A, B and C on the testing board (Fig. 2). (Discriminations (v) and (vi) were originally intended as training tasks to get the monkeys used to working in the dark with stimuli in varying positions for Discriminations (vii) and (viii)), and it was expected that they would have to be given shaping trials, for example by gradually dimming the house-lights down. In fact, all monkeys transferred immediately between tasks and no shaping trials were necessary.)

(vii) Landmark – Luminous stimuli – Fixed position. Two square luminous plaques covered food-wells B2 and B8, while a circular luminous plaque, the 'landmark', appeared in pseudorandom alternation over food-well C3 or C7 (Fig. 2). The food-well under the square plaque nearest to the landmark was baited. As in (v) and (vi), the lights in the Wisconsin Box were turned out during the trial so that the only visible objects were the 3 plaques.

(viii) Landmark – Luminous stimuli – Variable position. As Discrimination (vii), except that the two square plaques appeared pseudorandomly in any of the 7 positions B2–B8, with the constraint that there must always have been at least two uncovered food-wells between them which gave 10 possible combinations. The circular 'landmark' plaque appeared in any one of the 5 positions C3–C7, with the constraint that it must always have been between the two square plaques, but not equidistant from them, which gave an overall total of 26 different combinations of stimulus positions. In 24 of these 26 combinations, the landmark was in a position which could signify either left square positive or right square positive, depending on the relative positions of the 3 stimuli (Fig. 3). So, unlike previous landmark tasks, it was not possible for the monkey to use egocentric localisation to solve the problem, it was a purely allocentric task (see Introduction).

All randomisations between left and right were determined using a Gellermann pseudorandom sequence. Randomisations of positions over the testing board were determined by generating random sequences with the single constraint that each position should occur once before any position recurred. To make testing practicable, complete sequences did recur, but never within 200 trials (i.e. 5 test days), so that in Discrimination (viii), the variable position landmark test, the 26 possible combinations of stimulus positions ran through 8 random sequences (208 trials) before the first sequence was repeated.

Both trials-to-criterion and errors-to-criterion
were recorded and all initial statistical analysis was done using the randomisation test. The probability (P) of obtaining scores greater than or equal to the observed difference between groups of conditions is given in each case and a value of \( P \leq 0.05 \) is taken to indicate that a difference is significant.

RESULTS

Overall preoperative performance. Summating the scores from all the preoperative tests, there were no differences between the experimental groups and the controls on either trials- or errors-to-criterion (IP vs C: Trials \( P = 0.40 \), Errors \( P = 0.45 \); FEF vs C: Trials \( P = 0.50 \), Errors \( P = 0.50 \)). However, the 3 cynomolgus monkeys (one in each group) did perform rather worse than the rhesus (Trials \( P = 0.024 \), Errors \( P = 0.012 \)).

Discriminations (i) to (iv) - stimuli in fixed positions in the light. Preoperatively, there were no differences between the experimental groups and the controls for any of the tests for either trials- or errors-to-criterion (\( P > 0.05 \) in every case). Postoperative performance is shown in Fig. 4. There was still no difference between the experimental and control groups on Discriminations (i) Black + vs White −, (ii) Left + vs Right − and (iv) Square + vs Circle − (\( P > 0.05 \) in all cases). On Discrimination (iii) Centre + vs Left −, Right −, the IP group was impaired (IP vs C: Trials \( P = 0.05 \), Errors \( P = 0.05 \)) while the FEF group was not (FEF vs C: Trials \( P = 0.10 \), Errors \( P = 0.10 \)).

Discriminations (v) and (vi) - luminous patterns in the dark. Preoperatively, there were no differences between the experimental groups and the controls (\( P > 0.05 \) in every case), and, postoperatively, all monkeys reached criterion in the minimum of 100 trials on both tests. However, postoperative errors did show an interesting pattern (Fig. 5). Comparing errors on the fixed and variable position tests, there were slight savings in the Control group and the IP group showed no change, but the performance of the FEF group deteriorated when the two stimuli to be discriminated began appearing in different positions (Increase in Errors from Fixed position to Variable position: FEF > C, \( P = 0.05 \); IP = C, \( P = 0.50 \); FEF > IP, \( P = 0.05 \)).

Discriminations (vii) and (viii) - landmark tests. Preoperatively, there was considerable variation between monkeys, although the only significant difference between groups was that the IP group reached criterion faster than the Control group on Discrimination (viii), the variable position condition (Trials \( P = 0.05 \), Errors \( P = 0.05 \)). Because of this individual variation, group comparisons were done on the pre- to postoperative change in performance for each monkey (Fig. 6).

On discrimination (vii), luminous stimuli in a
Trials to criterion

0 100 200 300 400 500 600
C FEF IP C FEF IP C FEF IP C FEF IP
Black/White Left/Right Centre Circle/Square (i) (ii) (iii) (iv)

Errors to criterion

0 100 200 300 400 500 600
C FEF IP C FEF IP C FEF IP C FEF IP
Fixed position Variable position (v) (vi)

Fig. 4. Postoperative performance (means and S.E.s) of the 3 groups on Discriminations (i) to (iv). (a): trials to criterion. (b): errors to criterion.

Fig. 5. Postoperative performance (means and S.E.s) of the 3 groups on Discriminations (v) and (vi) – Luminous patterns in the dark.

fixed position, all groups showed postoperative savings and there were no differences between them ($P > 0.05$ in every case).

On Discrimination (viii), luminous stimuli in variable positions, both IP and FEF lesions produced a decrement in performance compared with the Control group ($P = 0.05$ in every case). Although the decrement was larger for IP lesions than for FEF lesions (Fig. 6), this difference was not significant (Trials $P = 0.10$, Errors $P = 0.10$). However, the difference between the variable and the fixed condition was significantly greater than in the Control group for the IP group but not for the FEF group (IP vs C: Trials $P = 0.05$, Errors $P = 0.05$; FEF vs C: Trials $P = 0.15$, Errors $P = 0.25$), suggesting that changing to the variable position condition was more disrupting for the IP group than for the FEF group.

Perseveration. The possibility that the FEF group’s deficit in Discrimination (viii), landmark with luminous stimuli in variable positions, might be due to response perseveration was tested by examining the first 100 postoperative trials. The mean percentage of errors which were repetitions of an error on the previous trial were: Control $53.7 \pm 10.6$; FEF $59.5 \pm 15.3$; IP $62.8 \pm 9.5$ (They were responding to different places on each trial, so a repetition would indicate perseveration.
not of a movement but of a response strategy.) None of the differences between the groups was significant (FEF vs C, \( P = 0.40 \); IP vs C, \( P = 0.25 \); FEF vs IP, \( P = 0.45 \)).

**Spatial discriminability and cue–response separation.** The first 100 trials on landmark Discrimination (viii) were also analysed to determine the effects of variations of stimulus layout on performance. Because the distance between the two square plaques and the position of the circular, 'landmark' plaque were both varying (Fig. 3), it was possible to analyse separately the effects of discrimination difficulty and cue–response separation. The variation of performance with discrimination difficulty is shown in Fig. 7. An ANOVA showed that there was a clear improvement in performance as discriminability increased \( (F_{3,18} = 17.71, P < 0.001) \). Although there was no significant difference between the groups at this

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**Fig. 6.** Pre- to postoperative change in performance (means and S.E.s) of the 3 groups on Discriminations (vii) and (viii) Landmark tests. a: trials to criterion. b: errors to criterion.

**Fig. 7.** The effect of varying spatial discriminability on the performance of the 3 groups on Discrimination (viii) Landmark test – Variable position. (Per cent spatial discriminability is defined as \( 100 \frac{(D_1 - D_2)}{(D_1 + D_2)} \), where \( D_1 \) is the distance along the left-right axis between the circular Landmark and the further, negative, square plaque and \( D_2 \) is the distance between the Landmark and the nearer, positive, square plaque.)
TABLE I

Effect of varying cue-response separation on performance in the variable position landmark task – Discrimination (viii)

Percentage (mean ± S.E.M.) of trials at each separation on which an error was made.

<table>
<thead>
<tr>
<th>Group</th>
<th>Cue-response separation (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7</td>
</tr>
<tr>
<td>Control</td>
<td>15.2 ± 2.0</td>
</tr>
<tr>
<td>IP</td>
<td>22.1 ± 4.7</td>
</tr>
<tr>
<td>FEF</td>
<td>22.5 ± 7.9</td>
</tr>
</tbody>
</table>

stage, there was a small interaction between groups and discriminability \( F_{6,18} = 3.51, P < 0.05 \). There were two levels of cue–response separation: 7 cm and 14 cm (Fig. 3). Table I shows the performance of the 3 groups at these two separations. There was no effect of separation on performance \( F_{1,6} = 2.67, P > 0.05 \), nor was there an interaction between groups and separation \( F_{2,6} = 4.62, P > 0.05 \). The only group to show a worse performance with the larger separation was the control group. So, whereas spatial discriminability was a factor in determining the performance of the experimental groups, cue–response separation was not.

DISCUSSION

Both inferior parietal lobule lesions and frontal eye-field lesions produced impairments on the landmark test with a suggestion in the data that the inferior parietal deficit was more severe than the frontal eye-field deficit. This contradicts the view that the landmark task is a specific test of parietal function\(^{29,35}\) and confirms those authors\(^{1,22,23}\) who have also found it impaired after frontal lesions.

The parietal lesions in the present study were smaller than those used in previous experiments, being limited to Area PG, and unusually there was a deficit in simple retention of the task, without a reversal, so it is possible to conclude for the first time that Area PG is necessary for normal performance of the landmark task. The posterior bank of superior temporal sulcus, damaged along with Area PG in all previous studies, may or may not also be involved, but it is clearly not exclusively involved. Similarly, the present study shows that frontal eye-field lesions alone are sufficient to produce a deficit. It is not necessary to include the more anterior dorsal convexity along sulcus principalis which has been damaged in all previous studies. Perhaps because of the smallness of the frontal lesion, there was no evidence that perseveration was contributing to the deficit in the landmark task as it seems to have done in Milner’s study\(^{23}\).

The difference between the parietal and the frontal deficit was, contrary to Pohl’s original findings with the landmark task, basically quantitative. However, there is a hint of a more qualitative distinction in the finding that changing from fixed to variable stimulus positions resulted in an increase in errors in the inferior parietal group but not in the frontal eye-field group. This was not due to movement per se, since the parietal group was less disturbed than the frontal group when the stimuli were moved around in the non-spatial luminous pattern discrimination (Discriminations (v) and (vi)). It would therefore seem to be due to a greater difficulty in making relative position judgements allocentrically after inferior parietal than after frontal eye-field lesions. (The variable position landmark task performed with luminous stimuli in the dark, unlike the fixed position landmark task in this study and indeed unlike the landmark tests of all previous studies, could only be solved allocentrically (see Introduction).)

Inferior parietal lesions also produced a deficit on a spatial task in which the central of 3 adjacent square plaques had to be selected (Discrimination (iii) Centre ‘vs Left –, Right – Fixed position). Though all spatial discriminations must involve some spatial separation of at least part of the cue from the response position, this task was designed to minimise cue–response separation, so its impairment makes it at least unlikely that cue–response separation is the only crucial factor in inferior parietal deficits as Mendoza and Thomas\(^{22}\) and Iwai\(^{12}\) have suggested. This conclusion is supported by the postoperative trial-by-trial error analysis on the landmark test which
found that the degree of cue–response separation was not a factor in determining the performance of the experimental groups. (It is of course possible in many cases to reverse the direction of cause and effect proposed by Mendoza and Thomas\textsuperscript{22}: deficits on tasks with cue–response separations might be \textit{caused} by allocentric spatial confusions making it difficult for the monkey to organise his behaviour adequately.) Misreaching was not seen in any of the monkeys during testing, so it could not have been the cause of the deficit in this or any of the other tests.

The slight deficit caused by the frontal eye-field lesions on the luminous pattern discrimination when the stimuli were moved round from trial-to-trial (Discrimination (vi)) is similar to that found after much larger dorsolateral frontal lesions by Brody and Pribram\textsuperscript{1} in automated tests where the stimuli to be discriminated or responded to also appeared in different positions from trial-to-trial. These rather surprising deficits are presumably due to difficulties in finding the stimuli because of the impairment in visual search abilities that occur after frontal eye-field lesions\textsuperscript{5,13,14,18}. It is also therefore possible that the deficit after frontal eye-field lesions on the landmark task which requires a systematic scanning of the display is due to visual search difficulties. The lack of deficit on the variable position discrimination (Discrimination (vi)) after parietal lesions is slightly puzzling, given that parietal lesions also produce visual search deficits\textsuperscript{13}. However, the lesions giving visual search deficits included the posterior bank of superior temporal sulcus and it may be that, as with neglect\textsuperscript{8,16}, this is the crucial area. If so, visual search difficulties would not be contributing to the parietal deficit on the landmark task in the present study.

The frontal eye-fields and the inferior parietal lobule are very closely connected anatomically\textsuperscript{26,27,33} and they seem to produce a very similar pattern of spatial deficits when lesioned. However, it is possible to see emerging the outline of a way of differentiating their roles in spatial behaviour, based on the complex pattern of results presented here and similar to the disassociation recently suggested by deficits in a very different kind of spatial behaviour, maze run-

\textsuperscript{34}. The frontal eye-fields are concerned with spatially organising responses to explore the environment, so lesions produce impairments in the variable position pattern discrimination (vi) and the variable position landmark discrimination (viii). The inferior parietal lobule is concerned more directly with the processing of spatial information and the perception of spatial relationships, so lesions produce impairments in the discrimination of centre (iii) and the variable position landmark discrimination (viii).

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