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Generalized deficits in visual selective attention after V4 and TEO lesions in macaques

Peter De Weerd,[1] Robert Desimone[2] and Leslie G. Ungerleider[1]
[1]Laboratory of Brain & Cognition, NIMH, Bethesda, MD 20892, USA
[2]Laboratory of Neuropsychology, NIMH, Bethesda, MD 20892, USA

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Abstract

To test the role of areas V4 and TEO in the attentional filtering of distracting information, we studied the effects of lesions in these areas, in monkeys discriminating target stimuli surrounded by irrelevant distracters. The lesions were restricted, such that a single visual field quadrant was affected by a V4 lesion alone, a TEO lesion alone, or a combined lesion in V4 and TEO, while one quadrant served as a normal control. The monkeys fixated a spot while discriminating the orientation, colour or motion of target stimuli presented extrafoveally in each quadrant. When the target was presented alone, discrimination deficits in the quadrants affected by the lesions were generally small. However, these deficits were substantially increased by surrounding the target with luminance, colour or motion distracters. The discrimination of target orientation was more impaired than the discrimination of target colour or motion, irrespective of distracter type. The discrimination of target motion was strongly affected only by motion distracters. The magnitude of the impairments increased with distracter strength and with the extent to which the distracters conveyed information conflicting with the target. Deficits in the quadrant affected by combined V4 and TEO lesions were twice as large as those in quadrants affected by V4 or TEO lesions alone. The results suggest that in the absence of V4 and TEO, information from both relevant and irrelevant stimuli is 'averaged' together across several different feature domains, impairing the discrimination of the relevant target features. The results suggest a broad role of V4 and TEO in visual selective attention.

Introduction

Neurophysiological studies (Haenny & Schiller, 1988; Motter, 1993, 1994; McAdams & Maunsell, 1999; Treue & Trujillo, 1999), imaging studies (Corbetta *et al*., 1990; Haxby *et al*., 1994; Shulman *et al*., 1997; Culham *et al*., 1998; Kastner *et al*., 1998, 1999; Mangun *et al*., 1998; Tootell *et al*., 1998; O'Craven *et al*., 1999; Hopfinger *et al*., 2000; Martinez *et al*., 2001) and studies measuring event-related brain potentials (Luck *et al*., 1994; Anllo-Vento & Hillyard, 1996; Morgan *et al*., 1996; Luck *et al*., 2000) have established that visual responses are modulated by attention in extrastriate cortex, and some degree of attentional modulation in V1 has been reported as well (Haenny & Schiller, 1988; Motter, 1993; Roelfsema *et al*., 1998; Ress *et al*., 2000). Furthermore, neurophysiological studies in ventral stream areas, important for object recognition, have shown that when two stimuli are presented within the same receptive field (RF), neuronal responses in the absence of attention are determined largely by the strongest stimulus. Attention, however, can switch control of the cell's response to the behaviourally relevant stimulus, although that stimulus may be the weakest (Moran & Desimone, 1985; Chelazzi *et al*., 1993; Luck *et al*., 1997; Reynolds *et al*., 1999, 2000; Fries *et al*., 2001). This may reflect a top-down biasing of competition among multiple stimuli, allowing the behaviourally relevant stimulus to overcome competition from strong, but behaviourally irrelevant, distracters (Desimone & Duncan, 1995). Similar mechanisms operate in the dorsal stream (Treue & Maunsell, 1996, 1999), which contributes to motion and spatial perception.

Neurophysiological and imaging studies cannot determine whether an observed neural response is necessary for a particular behaviour. Yet, few behavioural studies have investigated the effects of extrastriate lesions on the discrimination of targets presented among distracters. Notable exceptions are the studies by Schiller & Lee (1991) and Schiller (1993), which demonstrated temporary deficits in the detection of a target among distracters after V4 lesions. Furthermore, De Weerd *et al*. (1999) found that small-to-moderate deficits in grating orientation discrimination observed without distracters were greatly exacerbated by the addition of luminance-defined distracter disks around the target in parts of the visual field affected by lesions in V4 and/or TEO. When the target contrast was increased to exceed distracter contrast, the detrimental effect of the distracters on target discrimination was reduced, indicating that perception was dominated by the stimulus defined by the highest luminance contrast. Related data were reported by Gallant *et al*. (2000) in a human patient with a V4 lesion. Together, these data suggest that V4 and TEO are sites where top-down attentional inputs boost the effective contrast of a behaviourally relevant target object compared with that of distracters, allowing the target to gain control over visual processing in downstream areas (attentional selection of the target).

As pointed out by Merigan (1999), there is not yet behavioural evidence for such a role of V4 and TEO in the attentional selection of targets defined in stimulus domains other than luminance. We tested therefore whether areas V4 and TEO play a general role in selective

Correspondence: Dr P. De Weerd, at *present address below.
E-mail: pdeweerd@u.arizona.edu

**Present address*: University of Arizona, College of Social and Behavioural Sciences, Department of Psychology (Bldg 68), 1503 E. University Blvd, PO Box 210068, Tucson, AZ 85721-0068, USA.

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attention, by assessing lesion-induced selective attention deficits with targets and distracters defined not only by luminance, but also by colour and motion.

Materials and methods

Subjects and lesions

The two monkeys (M1, id# 86042, and M2, id# RDG2) from De Weerd *et al*. (1999) were used in the current experiments. Both were male and weighed approximately 10 kg. All surgery and behavioural testing was conducted according to NIH guidelines. Surgery was conducted under full anaesthesia [3–5% isofluorane in oxygen gas, after sedation with ketamine hydrochloride (10 mg/kg i.m.) and intubation], and all possible measures were taken to maintain health and comfort throughout the entire period of experimentation.

Implant surgery involved the placement of a post to immobilize the head and the introduction of an eye-coil in the sclera to monitor eye movements (Robinson, 1963). Details of lesion surgery have been described elsewhere (De Weerd *et al*., 1996, 1999). The lesion in the dorsal part of V4 in the left hemisphere affected the lower, contralateral quadrant of the visual field (Gattass *et al*., 1988). In the right hemisphere, the lesion in dorsal V4 was extended to include all of area TEO, which therefore affected the entire contralateral hemifield (Boussaoud *et al*., 1991), in addition to the contralateral lower quadrant affected by the lesion in dorsal V4. This resulted in the distribution of affected quadrants shown in Fig. 1. This lesion approach permits a comparison of several lesion conditions against baseline measurements within the same animal. Given this sensitive, within-subject design, we estimated that extensive measurements in two monkeys would be sufficient to complete the study.

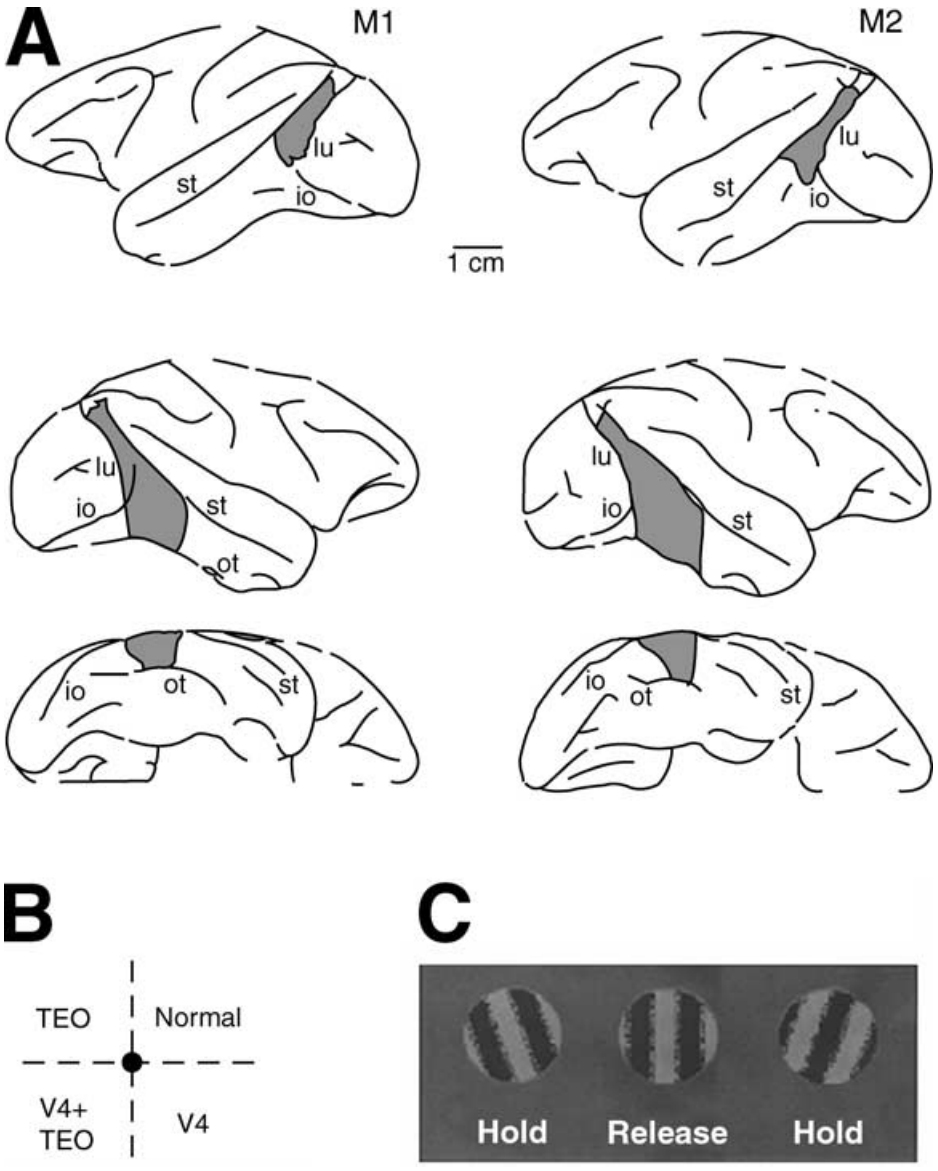

FIG. 1. Extent of V4 and TEO lesions in monkeys M1 and M2. (A) Lateral view of the left hemisphere showing a lesion (in dark shading) in the dorsal part of V4 for monkeys M1 and M2, shown on top. Below are lateral and ventral views of the right hemisphere showing a lesion in the dorsal part of V4 and in TEO in M1 and M2. The MRI scans suggest unintended damage medial to the occipital temporal sulcus (ot) in monkey M2 (lighter shading). Abbreviations: io, inferior occipital sulcus; lu, lunate sulcus; ot, occipital temporal sulcus; st, superior temporal sulcus. (B) Distribution of lesion effects in the four quadrants of the visual field, derived from retinotopy in areas V4 and TEO (see Materials and methods for explanation). (C) Example of a 'go' stimulus (vertical grating) and two 'no-go' stimuli used in the orientation discrimination task. For a description of other tasks, see Materials and methods. This figure was reproduced from De Weerd *et al*. (1999).

Lesion reconstruction was based on structural coronal slices obtained with MRI (GE 1.5T, thick 1 mm, 256 × 160 or 256 × 192 matrix, 4NEX, FOV 10–11 cm). In monkey M1, the lesions were as intended. In monkey M2, the V4 lesions were as intended, but the TEO lesion encroached anteriorly into area TE, and medially it appears that there was some extension into the parahippocampal gyrus (see Fig. 1).

Stimuli, task, threshold measurements and data analysis

The animals were seated in a primate chair and viewed a colour monitor at 57 cm. They were trained to grab a metal lever to turn on a small central red spot, to fixate it and to discriminate stimuli presented extrafoveally in one of the four visual field quadrants. Standard eccentricity of the stimuli was 5.8°. Trials with eye movements outside a 1.5°-sq window centred on fixation were aborted. The standard luminance of the screen's background was 10.8 cd/m^2 in M1 and 12 cd/m^2 in M2. Because colour and luminance varied with the temperature of the monitor, experiments were started and measurements were taken after the monitor had been on for at least 30 min. Stimulus and background luminances and colours were re-calibrated frequently using a Minolta spot luminance meter.

Stimuli were presented for 600 ms. During the 1200 ms following stimulus onset, the monkey was rewarded with orange juice for releasing the lever when a fixed reference stimulus was presented ('go' stimulus), and for holding the lever when a variable comparison stimulus was presented ('no-go' stimulus). Correct responses were rewarded with orange juice.

Except for the acuity task (see below), thresholds were measured using an adaptive method in which the difference between 'go' and 'no-go' stimuli was diminished (usually proportionally) after four consecutive correct responses, and increased after a single incorrect one. Using this staircase method, the stimulus differences converge around a level that corresponds to 84% correct performance (Wetherill & Levitt, 1965). The threshold measurement was terminated after a maximum of 120 trials or after 14 reversal points. The 84% correct threshold was calculated as the geometric mean of all reversal points, except the first four, such that each threshold was based on approximately 100 trials.

A typical testing session consisted of four consecutive threshold measurements in each quadrant, with the order between quadrants randomized over sessions. During a single session, one experimental condition was tested in all four quadrants (total of 16 thresholds). Both monkeys executed up to three testing sessions daily, and the experimental condition in each session was picked randomly.

Lesion effects were measured by comparing performance in the normal quadrant with performance in the three lesion-affected quadrants. Data were analysed using random effects ANOVA and linear contrasts, and effects are described as significant when P-values were less than 0.05. Thresholds were log-transformed to homogenize variance, and percentages correct were Z-transformed. Thresholds obtained preoperatively showed no asymmetries between quadrants. All thresholds reported here were obtained after extensive postoperative training caused performance to asymptote in all quadrants. Reaction times were constant across conditions, and in the order of 500 ms. We found no differences in reaction times between normal and lesion-affected quadrants, which likely reflects the fact that the staircase procedure used to measure the thresholds equalized the difficulty level among quadrants.

Attention-related experiments

We tested the animal's ability to attend to the features of a target stimulus in the presence of distracter stimuli. Target stimuli (the 'go' and 'no-go' stimuli, described above) consisted of static gratings, static disks of different colours or moving patterns. For each of these target types, the effects of disk-shaped luminance, colour and motion distracters were tested, resulting in nine combinations of different target and distracter types. Both targets and distracters were disk-shaped and were presented in close proximity to one another (0.2° gap between target and distracters). In all experiments, distracters were shown in triplets and, unless mentioned otherwise, their arrangement around the target was chosen randomly in each trial from eight predefined configurations. The position of the target stimulus remained fixed from trial to trial.

The luminance of grating and colour targets, and of colour and motion distracters was matched as closely as possible to the background's luminance (see below). Due to chromatic aberrations in the case of colour stimuli, and to limitations in the precision of luminance measurements in general, perfect equiluminance is impossible to achieve. Nevertheless, we contend that the functional significance of any cue related to small deviations from equiluminance in the above-mentioned stimuli was very small compared with the large experimental variation of the distracters' luminance, colour saturation or motion signal, and we therefore consider it appropriate to describe those stimuli as 'equiluminant'.

Discrimination tasks and target stimuli

Orientation discrimination of luminance-defined gratings. The orientation of the 'go' stimulus in the orientation task was vertical, and any stimulus with an orientation other than vertical was a 'no-go' stimulus (Fig. 1C). Square-wave, phase-randomized gratings with a low spatial periodicity (1.1 c/deg in M1 and 0.6 c/deg in M2) were presented in a circular aperture (2.2° in M1 and 4.4° in M2) at the standard eccentricity of 5.8°. The edges of the grating stimulus consisted of a 0.1° wide band of random noise (50% pixels randomly turned on or off), which masked the artefacts associated with the presentation of orientations close to the principal axes on a digitized screen. Standard grating contrast was 50%. To calculate grating contrast, a Michelson index was used in which the luminance of the dark stripes was subtracted from the luminance of the white stripes, and the result expressed as a percentage of the sum of the two luminances. The average luminance of the grating matched that of the grey background.

During staircase threshold measurements, the orientation difference between the vertical grating ('go' stimulus) and comparison gratings ('no-go' stimuli) was adapted to performance proportionally by multiplying or dividing the current orientation difference by a factor of 1.25. Twenty orientation differences were used varying between 1.3° and 90°.

Colour discrimination of blue vs. green. The colour of the 'go' stimulus for the colour task was blue, and any stimulus with a colour that was a mixture of green and blue was a 'no-go' stimulus. Coloured stimuli were presented in a 2.2° circular aperture. The variable colour stimuli were calibrated so they would fall on a straight line in CIE colour space between a pure blue and a pure green. Careful measurements were carried out to closely match the luminance of the colour stimuli with the luminance of the background. The colour stimuli were calibrated to ensure that any deviations from perfect equiluminance never exceeded 0.1 cd/m^2. This contrast cue (0.5% against the background) is unlikely to be above detection threshold, and could not have contributed to the colour discriminations because it was equally present in standard and variable stimuli. During the staircase measurements, the colour of the variable stimuli was adapted to performance by using a small proportional step-size of approximately 1.05 between neighbouring colours in CIE space. Figure 2 (solid symbols) shows the standard and variable stimuli plotted in CIE colour space.

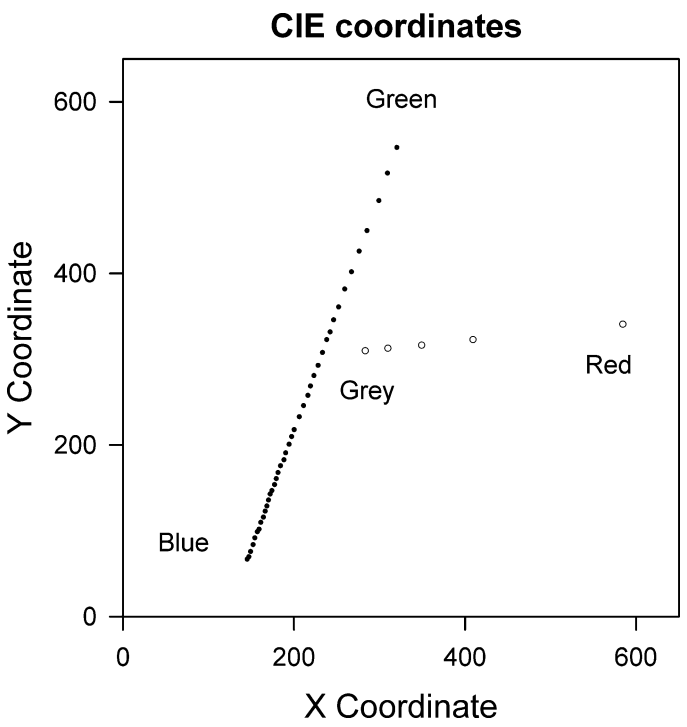

FIG. 2. CIE colour coordinates used to vary colour targets along the blue–green colour axis (solid symbols), and to vary the saturation of red distracters (open symbols). In different re-calibrations, position of individual dots could vary slightly.

Motion discrimination. In the motion task, motion was directed upward vertically in the 'go' stimulus, and left or rightward horizontally in 'no-go' stimuli. Stimuli consisted of a dark disk, 2.2° in diameter, which was overlaid with 15% white pixels moving in incoherent directions (noise) and other white pixels moving in a coherent direction (signal). The contrast between the pixels and the disk was 87% (Michelson index), and the pixels were 0.08° by 0.08° in size. Had the disk been filled with 50% white pixels, the stimulus would have been equiluminant with the grey background. Because the stimuli contained less than 50% pixels, the average luminance of the stimuli was less than that of the background. During a single presentation of the motion stimulus, 36 frames were played at 60 Hz (600 ms total duration). Between 1% and 20% signal pixels were added on top of the noise (15%). Each signal pixel moved coherently in a given direction from frame to frame, until it was terminated, at which point a new signal pixel was born in a randomly chosen location in the display. The chance for a signal pixel to be terminated was 20% on each frame, such that approximately 90% of the pixels were replaced after 10 frames. The chance for a noise pixel to be terminated was 50% on each frame.

During the staircase measurements, the monkeys discriminated the two orthogonal directions of motion, while the difficulty of the task was adapted to performance by varying signal strength in the motion targets. Signal strength of both the 'go' and 'no-go' stimuli was varied in steps of 1%, up to a signal strength of 10% signal pixels, and in steps of 2%, up to 20% signal pixels. Note that a variation in percentage signal pixels was associated with a corresponding variation in the global luminance of the target. Because the global luminance of the target was equal for 'go' and 'no-go' stimuli at each signal strength, this luminance variation could not be used as a cue to solve the task.

Distracter stimuli

Luminance distracters. Luminance distracters were disks of the same size as the target. They were darker or brighter than the background, and their strength was manipulated by varying contrast. To calculate distracter contrast, the luminance of the grey screen background was subtracted from the luminance of the distracters, and the result expressed as a percentage of the sum of those two luminances (Michelson index). The resulting contrasts for bright distracters were 5%, 10%, 20% and 50%; and the resulting contrasts for dark distracters were −5%, −10%, −20% and −50%. Experiments in which the contrast of distracters was increased up to 100% did not reveal additional impairments in orientation discrimination beyond those obtained with 50% contrast gratings (unpublished data). This suggests that at a contrast of 50% (or −50%) the effect of luminance distracters is maximized.

Colour distracters. Colour distracters were red disks of the same size as the target stimulus. The strength of the distracters was manipulated by changing colour saturation while closely matching the luminance of the distracters to that of the background, following the same procedures as described for colour targets. Colour progression in CIE space was approximately on a straight line. Colour steps were chosen such that the weakest distracter would be removed from grey by a distance in CIE space equal to 10% of the total distance between grey and pure red. To increase distracter strength, this distance was set to 20%, 40% and 100% (see open symbols in Fig. 2). Saturation was increased up to 100%, because pilot measurements in the V4 + TEO-affected quadrant indicated that grating orientation thresholds (50% luminance contrast) increased strongly as saturation of the colour distracters was increased from 50% to 100%. Hence, while a 50% luminance contrast maximized the effects of luminance distracters, a 100% colour saturation was required to maximize the effect of colour distracters. The colour saturation levels of 10%, 20%, 40% and 100% match the relative difference between the luminance contrast levels of luminance distracters (e.g. 5%, 10%, 20% and 50% for the bright distracters).

Motion distracters. Motion distracters were movies made of 36 frames of 50% random noise, with square pixels of 0.8° by 0.8°, played at 60 Hz. To manipulate the strength of the distracters, the contrast between darker and brighter pixels (Michelson index) was manipulated in the same four steps used for luminance distracters (5%, 10%, 20% and 50%), and pilot data indicated that 50% was at saturation level. The overall luminance of the distracters was matched to the background's luminance for all distracter strengths.

Additional distracter manipulations. Using the grating orientation discrimination task, two experiments were carried out that examined specific interactions between the grating target and luminance distracters (see Results). Gratings were 2.2° in diameter in both monkeys. In the first experiment, there were three distracter conditions. In the first condition, a target grating was surrounded with disk-shaped distracters, as in preceding experiments. In the second condition, three square-shaped distracters were used in an upright orientation. In the third condition, 44 randomly orientated, small squares were used as distracters. The total surface area of the square distracters in both conditions equalled that in the standard condition (three disks of 1.1° radius; total surface area is 11.4° squared). The small squares (each 0.5° by 0.5° in size) were confined to a 7° by 7° square region, centred on the middle of the target. Position randomization of the individual elements was within 25% of the distance between elements if they had

TABLE 1. Chronology of postoperative testing

Months postop.	MONKEY M1				MONKEY M2			
	Date	Target	Distracter	Fig./Table	Date	Target	Distracter	Fig./Table
1	Jan-95	Various shapes		**	Nov-96	Grating training	Luminance	Fig. 9
						Grating		
2		+ versus T		Table 3	Dec-96†	Grating	Luminance	Figs 3, 6, 9
3		Grating training			Jan-97	No testing		
		Grating						
4		Colour training				No testing		
		Colour		**				
5		Triangle training			Mar-97†	Colour training		
		Triangle		**		Grating	Luminance	Fig. 9
		H versus U		Table 3				
6		Grating	Luminance	**		Colour	Luminance	Figs 3, 6
						Motion training		
7	Jul-95†	Grating	Luminance	Figs 3, 6, 9		Motion	Luminance	Figs 3, 6
8		No testing				No testing		
9		No testing				Colour training		
						Colour triangle		**
10		No testing				Acuity		Table 3
						+ versus T		Table 3
11		No testing				Grating	Luminance	**
						Grating	Distracter-shape	Fig. 7
12	Dec-95†	Grating	Luminance	Fig. 9**	Oct-97†	Grating	Luminance	Fig. 9**
						Motion training		
13	Jan-96	Colour	Luminance	Figs 3, 6		Motion	Motion	Figs 5, 6
		Motion training				Grating	Motion	Figs 5, 6
14		Motion	Luminance	Figs 3, 6		Colour	Motion	Figs 5, 6
						Colour	Colour	Figs 4, 6
15		Grating	Colour	Figs 4, 6	Jan-98	Grating	Colour	Figs 4, 6
						Motion	Colour	Figs 4, 6
16		Grating	Motion	Figs 5, 6				
17		Motion	Motion	Figs 5, 6				
		Motion	Colour	Figs 4, 6				
18	Jun-96†	Colour	Motion	Figs 5, 6				
		Colour	Colour	Figs 4, 6				
		Grating	Luminance	Fig. 9				
19		Acuity		Table 3**				
24	Jan-97†	Grating	Distracter-shape	Figs 7, 9				
66	Jun-00†	Grating	Luminance	Fig. 9				
90	Jun-02†	Grating	Grating-distracter	Figs 8, 9				

In monkey M1, training started on 17 March 1994, the lesion was placed on 9 January 1995, and postoperative testing started on 21 January 1995. In M2, training started on 26 December 1995, the lesion was placed on 1 October 1996, and postoperative testing started on 26 November 1996. Target and distracter (if applicable) are indicated for each postoperative experiment for both monkeys, and figures or tables presenting the data are referred to. 'No testing' indicates periods without testing, due to eye-coil surgery, or technical or other difficulties. †Months during which measurements were collected with target gratings and disk-shaped luminance distracters of 50% contrast, included in Fig. 9. **Postoperative experiments, during which additional data were collected that are not part of the present paper. Specifically, during postoperative months 1, 4 and 5 in monkey M1, and month 9 in monkey M2, the spatial generalization of shape and colour discriminations was tested in lesion-affected and normal quadrants (De Weerd *et al*., 2003). During months 6, 12 and 19 in M1, and months 11 and 12 in M2, manipulations of grating and distracter contrast, and target-distracter distance were carried out, as well as a target detection experiment and an acuity measurement (De Weerd *et al*., 1999; acuity data summarized in Table 3).

been presented on a regular grid (0.25°). Hence, the orientation and position of the individual elements varied from trial to trial. The internal contrast of the target grating as well as the contrast between luminance distracters and background were 50%. In the second experiment, there were again three distracter conditions. In the first condition, a target grating was surrounded by three disk-shaped luminance distracters. In the second condition, randomly orientated grating distracters were used as distracters (random distracter-orientation condition). In the third condition, the orientation of grating distracters matched the orientation of the target on each trial (the parallel distracter-orientation condition). In this experiment, all distracters were presented in three fixed locations at eccentricities that exceeded the eccentricity of the target. This arrangement avoided a possible enhancement of target discrimination performance in the parallel distracter-orientation condition due to the presentation of an informative stimulus close to fixation in the parallel distracter-orientation condition (see Results). At the same time, this distracter arrangement limited the possibilities for randomization of distracter position, and we therefore presented a constant, regularly spaced configuration in all discrimination trials. As in the previous experiment, the contrast of all gratings was 50%.

Attention deficit index

In a number of experiments, an attention deficit index (ADI) was used to quantify the effects of distracters in each lesion-affected quadrant. The ADI is the logarithm of the ratio between the threshold (*THR*) in a lesion-affected quadrant (L) obtained with distracters (d) (symbolized as THR_{Ld}) and the threshold in the same lesion-affected quadrant obtained without distracters (THR_L), minus the logarithm of the ratio between the threshold in the normal quadrant obtained with distracters (THR_{Nd}) and the threshold in the normal quadrant obtained without distracters (THR_N), as shown below:

$$\mathrm{ADI} = \log\left(THR_{Ld}/THR_L\right) - \log\left(THR_{Nd}/THR_N\right)$$

TABLE 2. Results of statistical tests referred to in the text

Distracter	Target	Entry	Effect	M1	M2
Luminance	Grating	1	Quadrant (Q)	$F_{3,155} = 197.800$, $P < 0.001$	$F_{3,80} = 447.058$, $P < 0.001$
		2	Distracters (D)	$F_{8,155} = 17.972$, $P < 0.001$	$F_{6,80} = 12.641$, $P < 0.001$
		3	Interaction (Q * D)	$F_{24,155} = 5.034$, $P < 0.001$	$F_{18,80} = 5.312$, $P < 0.001$
		4	(Q1,D5) = (Q1,D1–4)	$F_{1,155} = 0.122$, $P = 0.727$	–
		5	(Q1,D5) = (Q1,D6–9)	$F_{1,155} = 0.114$, $P = 0.736$	–
		6	(Q1,D5) = (Q1,D2–4)	–	$F_{1,80} = 0.414$, $P = 0.522$
		7	(Q1,D5) = (Q1,D6–8)	–	$F_{1,80} = 2.336$, $P = 0.130$
	Colour	8	Quadrant (Q)	$F_{3,168} = 49.804$, $P < 0.001$	$F_{3,238} = 473.415$, $P < 0.001$
		9	Distracters (D)	$F_{8,168} = 15.687$, $P < 0.001$	$F_{8,238} = 24.185$, $P < 0.001$
		10	Interaction (Q * D)	$F_{24,168} = 2.198$, $P = 0.002$	$F_{24,238} = 5.232$, $P < 0.000$
		11	(Q1,D5) = (Q1,D1–4)	$F_{1,168} = 0.013$, $P = 0.921$	$F_{1,238} = 0.069$, $P = 0.793$
		12	(Q1,D5) = (Q1,D6–9)	$F_{1,168} = 0.006$, $P = 0.936$	$F_{1,238} = 0.326$, $P = 0.569$
	Motion	13	Quadrant (Q)	$F_{3,175} = 30.174$, $P < 0.001$	$F_{3,243} = 35.882$, $P < 0.001$
		14	Distracters (D)	$F_{8,243} = 12.093$, $P < 0.001$	$F_{8,175} = 1.613$, $P = 0.124$
		15	Interaction (Q * D)	$F_{24,243} = 1.262$, $P = 0.191$	$F_{24,175} = 1.243$, $P = 0.211$
Colour	Grating	16	Quadrant (Q)	$F_{3,59} = 94.886$, $P < 0.001$	$F_{3,109} = 1014.814$, $P < 0.001$
		17	Distracters (D)	$F_{4,59} = 26.307$, $P < 0.001$	$F_{3,109} = 14.213$, $P < 0.001$
		18	Interaction (Q * D)	$F_{12,59} = 11.029$, $P < 0.001$	$F_{9,109} = 9.945$, $P < 0.001$
		19	(Q1,D1) = (Q1,D2–5)	$F_{1,59} = 1.210$, $P = 0.276$	–
		20	(Q1,D1) = (Q1,D2–4)	–	$F_{1,109} = 6.091$, $P = 0.015$
	Colour	21	Quadrant (Q)	$F_{3,112} = 8.291$, $P < 0.001$	$F_{3,120} = 219.445$, $P < 0.001$
		22	Distracters (D)	$F_{4,112} = 18.007$, $P < 0.001$	$F_{4,120} = 18.760$, $P < 0.001$
		23	Interaction (Q * D)	$F_{12,112} = 3.186$, $P = 0.001$	$F_{12,120} = 3.74$, $P < 0.001$
		24	(Q1,D1) = (Q1,D2–5)	$F_{1,112} = 1.215$, $P = 0.273$	$F_{1,120} = 0.341$, $P = 0.560$
	Motion	25	Quadrant	$F_{3,12} = 2.390$, $P = 0.078$	$F_{3,12} = 316.117$, $P < 0.001$
		26	Distracters	$F_{4,12} = 2.068$, $P = 0.097$	$F_{4,12} = 1.950$, $P = 0.106$
		27	Interaction (Q * D)	$F_{12,59} = 0.285$, $P = 0.990$	$F_{12,121} = 0.018$, $P = 0.029$
		28	(Q3,D4) = (Q3,D5)	–	$F_{1,121} = 7.205$, $P = 0.008$
		29	(Q4,D4) = (Q4,D5)	–	$F_{1,121} = 4.939$, $P = 0.028$
		30	(Q1,D1) = (Q1,D2–5)	–	$F_{1,121} = 8.793$, $P = 0.004$
Motion	Grating	31	Quadrant (Q)	$F_{3,135} = 64.102$, $P < 0.001$	$F_{2,81} = 331.544$, $P = 0.004$
		32	Distracters (D)	$F_{4,135} = 68.830$, $P < 0.001$	$F_{3,81} = 4.713$, $P = 0.004$
		33	Interaction (Q * D)	$F_{12,135} = 6.764$, $P < 0.001$	$F_{6,81} = 5.451$, $P < 0.001$
		34	(Q1,D1) = (Q1,D2–5)	$F_{1,135} = 3.152$, $P = 0.078$	$F_{1,81} = 3.671$, $P = 0.061$
	Colour	35	Quadrant (Q)	$F_{3,97} = 20.723$, $P < 0.001$	$F_{3,125} = 299.874$, $P < 0.001$
		36	Distracters (D)	$F_{4,97} = 13.506$, $P < 0.001$	$F_{4,125} = 12.636$, $P < 0.001$
		37	Interaction (Q * D)	$F_{12,97} = 5.107$, $P < 0.001$	$F_{12,125} = 3.989$, $P < 0.001$
		38	(Q1,D1) = (Q1,D2–5)	$F_{1,97} = 0.741$, $P = 0.391$	$F_{1,125} = 3.725$, $P = 0.056$
	Motion	39	Quadrant	$F_{3,118} = 21.440$, $P < 0.001$	$F_{2,122} = 165.306$, $P < 0.001$
		40	Distracters	$F_{4,118} = 44.754$, $P < 0.001$	$F_{4,112} = 14.607$, $P < 0.001$
		41	Interaction (Q * D)	$F_{12,118} = 4.490$, $P < 0.001$	$F_{8,112} = 4.148$, $P < 0.001$
		42	(Q1,D1) = (Q1,D2–5)	$F_{1,118} = 8.032$, $P = 0.005$	$F_{1,112} = 0.019$, $P = 0.892$

Distracter	Target	Entry	Effect	M1 & M2 pooled data
Motion	Motion	43	Target Type (T)	$F_{2,78} = 19.184$, $P < 0.001$
		44	Distracter Type (D)	$F_{2,78} = 2.696$, $P = 0.074$
		45	Distracter Strength (S)	$F_{3,78} = 30.018$, $P = 0.003$
		46	Lesion Size (L)	$F_{1,78} = 33.404$, $P < 0.001$
		47	Interaction (D * T)	$F_{4,78} = 3.577$, $P = 0.010$
		48	Interaction (S * T)	$F_{6,78} = 2.273$, $P = 0.045$
		49	Interaction (S * L)	$F_{3,78} = 3.312$, $P = 0.024$
		50	T1 = T2	$F_{1,78} = 13.237$, $P < 0.001$
		51	T1 = T3	$F_{1,78} = 37.953$, $P < 0.001$
		52	T2 = T3	$F_{1,78} = 6.362$, $P = 0.014$
		53	(D1,T1–2) = (D1,T3)	$F_{1,78} = 23.066$, $P < 0.001$
		54	(D2,T1–2) = (D2,T3)	$F_{1,78} = 14.877$, $P < 0.001$
		55	(D3,T1–2) = (D3,T3)	$F_{1,78} = 0.001$, $P = 0.982$
		56	Interaction (S * T)	$F_{3,54} = 0.894$, $P = 0.450$
		57	(T1,S1–2) = (T2,S1–2)	$F_{1,78} = 4.457$, $P = 0.038$
		58	(T1,S1–2) = (T3,S1–2)	$F_{1,78} = 6.049$, $P = 0.016$
		59	Interaction (T * M)	$F_{1,72} = 2.087$, $P = 0.131$
		60	Interaction (D * T * M)	$F_{4,72} = 2.266$, $P = 0.07$
		61	Interaction (S * T * M)	$F_{2,72} = 0.459$, $P = 0.634$
		62	Interaction (S * L * M)	$F_{1,72} = 1.097$, $P = 0.299$
		63	Interaction (D * M)	$F_{2,72} = 7.317$, $P < 0.001$
		64	(D1,M1) = (D1,M2)	$F_{1,72} = 0.945$, $P = 0.334$
		65	(D2,M1) = (D2,M2)	$F_{1,72} = 19.432$, $P < 0.001$
		66	(D3,M1) = (D3,M2)	$F_{1,72} = 4.872$, $P = 0.030$
		67	Interaction (L * M)	$F_{2,144} = 11.855$, $P < 0.001$

TABLE 2. continued

Distracter	Target	Entry	Effect	M1	M2
No distracters	Grating	68	Quadrant (Q)	$F_{3,58} = 6.595$, $P < 0.001$	$F_{3,73} = 189.849$, $P < 0.001$
		69	Q1 = Q2	$F_{1,58} = 19.611$, $P < 0.001$	$F_{1,73} = 62.707$, $P < 0.001$
		70	Q1 = Q3	$F_{1,58} = 3.145$, $P = 0.081$	$F_{1,73} = 284.952$, $P < 0.001$
		71	Q1 = Q4	$F_{1,58} = 4.049$, $P = 0.049$	$F_{1,73} = 482.504$, $P < 0.001$
	Colour	72	Quadrant (Q)	$F_{3,66} = 0.758$, $P = 0.521$	$F_{3,79} = 129.968$, $P < 0.001$
		73	Q1 = Q2	–	$F_{1,79} = 128.843$, $P < 0.001$
		74	Q1 = Q3	–	$F_{1,79} = 272.637$, $P < 0.001$
		75	Q1 = Q4	–	$F_{1,79} = 333.518$, $P < 0.001$
	Motion	76	Quadrant (Q)	$F_{3,73} = 2.305$, $P = 0.133$	$F_{3,77} = 38.171$, $P < 0.001$
		77	Q1 = Q2	–	$F_{1,77} = 0.922$, $P = 0.340$
		78	Q1 = Q3	–	$F_{1,77} = 76.857$, $P < 0.001$
		79	Q1 = Q4	–	$F_{1,77} = 12.038$, $P < 0.001$
Manipulation	Grating	80	Quadrant (Q)	$F_{3,250} = 301.190$, $P < 0.001$	$F_{3,114} = 428.035$, $P < 0.001$
Distracter-type		81	Distracter-type (D)	$F_{3,250} = 54.481$, $P < 0.001$	$F_{3,114} = 30.292$, $P < 0.001$
		82	Interaction (Q * D)	$F_{9,250} = 16.143$, $P < 0.001$	$F_{9,114} = 6.164$, $P < 0.001$
		83	(Q1,D1) = (Q1,D2–4)	$F_{1,250} = 8.783$, $P = 0.003$	$F_{1,114} = 1.225$, $P = 0.271$
		84	(Q1,D2–4) = (Q2,D2–4)	$F_{1,250} = 830.616$, $P < 0.001$	$F_{1,114} = 181.245$, $P < 0.001$
		85	(Q1,D2–4) = (Q3,D2–4)	$F_{1,250} = 188.428$, $P < 0.001$	$F_{1,114} = 668.334$, $P < 0.001$
		86	(Q1,D2–4) = (Q4,D2–4)	$F_{1,250} = 1019.974$, $P < 0.001$	$F_{1,114} = 906.001$, $P < 0.001$
		87	(D2,Q2–4) = (D3,Q2–4)	$F_{1,250} = 0.266$, $P = 0.607$	$F_{1,114} = 2.321$, $P = 0.130$
		88	(D2,Q2–4) = (D4,Q2–4)	$F_{1,250} = 8.836$, $P = 0.003$	$F_{1,114} = 6.130$, $P = 0.015$
		89	Quadrant (Q)	$F_{3,176} = 201.859$, $P < 0.001$	–
		90	Distracter-type (D)	$F_{3,176} = 117.858$, $P < 0.001$	–
		91	Interaction (Q * D)	$F_{9,176} = 19.057$, $P < 0.001$	–
		92	(Q1,D1) = (Q2–4,D1)	$F_{1,176} = 24.085$, $P < 0.001$	–
		93	(D1,Q2–4) = (D2,Q2–4)	$F_{1,176} = 54.595$, $P < 0.001$	–
		94	(D1,Q1) = (D2–4,Q1)	$F_{1,176} = 3.891$, $P = 0.050$	–
		95	(D2,Q2–4) = (D4,Q2–4)	$F_{1,176} = 45.496$, $P < 0.001$	–
		96	(Q1,D1) = (Q1,D3)	$F_{1,176} = 0.210$, $P = 0.648$	–
		97	(Q1,D4) = (Q2,D4)	$F_{1,176} = 2.723$, $P = 0.101$	–
		98	(Q1,D4) = (Q3,D4)	$F_{1,176} = 0.035$, $P = 0.862$	–
		99	(D1,Q1) = (D4,Q1–3)	$F_{1,176} = 34.800$, $P < 0.001$	–
		100	(Q4,D1) = (Q4,D4)	$F_{1,176} = 0.090$, $P = 0.765$	–
Acuity test	Grating	101	Quadrant (Q)	$F_{3,48} = 0.472$, $P = 0.703$	$F_{3,74} = 2.877$, $P = 0.042$
		102	Spatial Frequency (SF)	$F_{3,48} = 1.348$, $P = 0.270$	$F_{4,74} = 50.941$, $P < 0.001$
		103	Interaction (Q * SF)	$F_{9,48} = 0.612$, $P = 0.780$	$F_{12,74} = 2.047$, $P = 0.031$
		104	(SF15.6,Q1) = (SF15.6,Q2)	–	$F_{1,74} = 12.028$, $P < 0.001$
		105	(SF15.6,Q1) = (SF15.6,Q3)	–	$F_{1,74} = 21.880$, $P < 0.001$
		106	(SF15.6,Q1) = (SF15.6,Q4)	–	$F_{1,74} = 22.850$, $P < 0.001$
Pattern	+ vs T	107	Quadrant (Q)	$F_{3,56} = 251.802$, $P < 0.001$	–
Discrimination	H vs U	108	Q1 = Q2	$F_{1,56} = 492.707$, $P < 0.001$	$U_{3,5} = 2.032$, $P = 0.042$
		109	Q1 = Q3	$F_{1,56} = 96.853$, $P < 0.001$	–
		110	Q1 = Q4	$F_{1,56} = 569.302$, $P < 0.001$	–

The table lists main effects of quadrant, distracters and interaction between the two factors in all experiments. Conventions. For brevity, normal, V4-affected, TEO-affected and V4 + TEO-affected quadrants are referred to as Q1, Q2, Q3 and Q4, respectively. The quadrant conditions compared with linear contrasts are indicated by using Q1–Q4 to refer to one of the four quadrants. For example, the notation 'Q1 = Q2' indicates a linear comparison between marginal means of the quadrant factor. The notation D refers to a distracter condition. Luminance distracter contrasts of −50%, −20%, −10%, −5%, 0%, 5%, 10%, 20% and 50% are referred to as D1–D9, respectively, with D5 being the no-distracter condition (entries 1–15). Colour (entries 16–30) and motion distracters (entries 31–42) are numbered D1 (no distracters) to D5 (strongest saturation, or motion signal). To denote a comparison between means in specific cells of the experimental design, the means are specified by their coordinates. For example, for entry 4, the notation (Q1, D5) = (Q1,D1–4) indicates a comparison within the normal quadrant between the no-distracter condition and the average of all four dark luminance distracters (−50%, −20%, −10% and −5%). In the analysis of ADIs (entries 43–67), target type (T) refers to the grating (T1), colour (T2) and motion targets (T3). Distracter (D) types are luminance (D1), colour (D2) and motion distracters (D3). Distracter strengths (S) are numbered from weakest (S1) to strongest (S4). Factor L (lesion size) has two levels (single and V4 + TEO lesion; see text). Effects shown under entries 43–58 were obtained with pooled data from the two monkeys. Effects shown under entries 59–66 belong to an anova in which monkey (M) was introduced as a random factor, in addition to factors D, T, S and L. The effect shown in entry 67 belongs to an anova, in which D, T, S, L and M were used as random factors, and in which L (lesion type) had three levels (V4, TEO and V4 + TEO-affected quadrants). In this analysis, four-way and five-way interactions were not included in the model. In anovas that included M as a factor (entries 59–67), factor S had two levels (the two weakest vs. the two strongest distracter strengths), which was necessary to have sufficient data per condition. For the manipulation of distracter type (D) in Fig. 7 (entries 80–88), conditions without distracters, disk distracters, square distracters and small square distracter are referred to as D1–D4, respectively. For the manipulation of distracter type in Fig. 8 (entries 89–100), conditions without distracters, disk distracters, random grating distracters and parallel grating distracters are referred to as D1–D4, respectively. In entries 104–106 performance at the 15.6 spatial frequency (SF15.6) was compared between the normal and the three lesion-affected quadrants in M2. *Conditions excluded from analysis*. In a number of experiments, particular conditions could not be included in anova. Entries 6, 7: extreme distracter contrasts were not included in anova because 84% correct thresholds could not be determined for −50% and 50% luminance distracters. Entries 17, 18, 20: in M2, the 100% colour distracter condition was not included in the anova because the monkey did not reach 84% correct discrimination performance in that condition (and hence no threshold could be determined). Entries 31–34: in M2, the V4 + TEO-affected quadrant and the 50% distracter contrast conditions were not included in the analysis because discrimination performance did not reach the 84% level. Entries 39–42: in M2, the V4 + TEO quadrant was not included in the analysis because of conditions in which 84% correct discrimination performance could not be reached. Entries 43–67: M2 did not reach thresholds for maximum distracter strengths in the V4 + TEO-affected quadrant in five conditions. These conditions included the maximum strength luminance, colour and motion distracters in the grating orientation discrimination task. For calculation of the ADI, the threshold value was arbitrarily set at 90°, although the monkey would not have reached an 84% correct performance when tested at a constant difference of 90°. In addition, performance of M2 did not reach threshold in the motion task for the strongest two motion distracter conditions. The value entered into the calculation of the ADI was the largest percentage of signal dots used during the staircase (20%), although the monkey would not have reached an 84% correct performance when tested at that percentage of signal dots. Thus, five of the 106 ADIs (see Fig. 6) summarizing performance in M2 are likely to represent an underestimate of the actual deficit. Entry 107–110: no anova was carried out for pattern discrimination data in M2 because in the TEO- and V4 + TEO-affected quadrants no 84% correct thresholds could be determined. Entry 108: a Mann–Whitney U-test was carried out to compare performance in normal and V4-affected quadrants in M2.

A positive ADI indicates that the relative increase of the target discrimination threshold induced by distracters in a given lesion-affected quadrant is larger than any relative increase that the same distracters might induce in the normal quadrant (see below). The ADI could become negative if relative distracter-induced threshold elevations were larger in the normal than in lesion-affected quadrants, or if distracters caused target discrimination thresholds to decrease below thresholds measured without distracters in normal and/or lesion-affected quadrants.

In conditions where performance did not reach 84% correct, precluding the measurement of thresholds, we arbitrarily entered the largest stimulus difference used in the threshold measurement into the equation used to calculate the ADI. Accordingly, in these conditions, the ADI is an underestimate of the true deficit (see legend to Table 2, entries 43–58, under *conditions excluded from analysis*).

Additional perceptual experiments

Acuity task

To obtain an approximate measure of acuity, the monkeys were required to release the lever for a vertical square wave grating and to hold the lever for a grey stimulus that matched the grating's average luminance and size (2.2° diameter). The monkeys were trained in this task using square-wave gratings with spatial frequencies starting at 1 cycle/°. During testing, the spatial frequency was increased up to 16 cycles/° (for its fundamental component). Given limitations of the stimulus monitor, these high-frequency gratings were necessarily square wave. Viewing distance during the acuity task was 80 cm instead of the standard 57 cm used in the other experiments.

Pattern discriminations (+ vs. T, H vs. U)

Both monkeys were tested in a '+ vs. T' discrimination. The + served as the 'go' stimulus, and the T served as the variable 'no-go' stimulus, with a variable offset of the upper, horizontal line relative to the middle of the vertical line (at which point the variable stimulus would look exactly like the +). Thus, the monkeys were required to release the lever when the + was presented and to hold the lever when any of the variations of the T was presented.

Because the two lines composing the + were 2° long (width of 0.2°), the maximum offset was 1° (i.e. a T), and the minimum offset was 0° (i.e. a +). During the threshold measurement, the offset was adapted to performance by varying it between both extremes in a constant step-size of 0.04°.

Monkey M1 was also tested in a 'H vs. U' discrimination. The vertical line segments in the two stimuli were 2° long and 0.2° wide, and the horizontal line segment was 1° long and 0.2° wide. The H served as the 'go' stimulus, and the U was made the variable ('no-go') stimulus by varying the offset of the horizontal line in the H from the middle of the vertical legs between 1° (i.e. a U) and 0° (i.e. an H). The threshold offsets were determined as described for the previous pattern discrimination. For both pattern discriminations, the stimuli were white on a grey background (contrast of 87%).

Testing history

Both monkeys were trained preoperatively on orientation discrimination tasks (with grating and dotted lines), on a '+ vs. T' discrimination task, on the colour discrimination task and on the motion discrimination task. Despite differences in the chronology of postoperative testing (Table 1), the main results in the two monkeys were similar (see Results). Because of the multitude of tasks on which the monkeys were trained and tested, a long time interval typically elapsed between pre- and postoperative testing of a task. Thus, retention could not be used as a useful measure of lesion deficits.

Results

Throughout the Results section, the results of statistical tests are given in Table 2. The statistical tests in Table 2 are referred to by entry numbers in the text.

Target–distracter interactions within and across stimulus domains

Effects of luminance distracters on orientation, colour and motion discrimination

Figure 3 shows that luminance distracters induced large elevations of both orientation and colour thresholds in the lesion-affected quadrants, which became more pronounced when the luminance contrast of the distracters was increased. However, the distracters did not induce any elevation of motion thresholds. In addition, no distracter-induced threshold elevations were observed in the normal quadrant.

In the orientation discrimination task, we found highly significant main effects of quadrant tested and of distracter contrast (entries 1, 2), as well as a highly significant interaction between these two factors (entry 3), in both monkeys. The interaction resulted from the fact that increases in distracter contrast had a very large effect on thresholds in the V4 + TEO affected quadrant, a smaller effect in the quadrants affected by the individual lesions, and no effect in the normal quadrant. The absence of significant distracter effects in the normal quadrant was confirmed by linear contrasts comparing the thresholds with and without distracters in that quadrant (entries 4–7).

The pattern of results was similar in the colour discrimination task with luminance distracters. For both monkeys, there were significant main effects of quadrant and of distracter contrast, and a significant interaction between those two factors (entries 8–10). The interaction resulted from the large effects of distracter contrast on thresholds in the lesion-affected quadrants (with the size of the effect depending upon lesion condition), while again no significant effect was found in the normal quadrant (see entries 11, 12). Note that in both the orientation discrimination and the colour discrimination tasks, thresholds in the TEO-affected and V4 + TEO-affected quadrants were larger in M2 than in M1.

In contrast to the effect of luminance distracters in the orientation and colour discrimination tasks, there was little effect of luminance distracters in the motion discrimination task. The main effect of quadrant was significant in M1 and in M2 (entry 13), and the effect of distracter contrast on thresholds was significant in M1 but not in M2 (entry 14). However, in neither monkey did we find a significant interaction between quadrant and distracter contrast (entry 15), indicating that the effect of distracter contrast on thresholds in lesion-affected and normal quadrants was indistinguishable in this task.

Effects of colour distracters on orientation, colour and motion discrimination

Figure 4 shows the findings with colour distracters, which were similar to the findings obtained with luminance distracters. We increased the saturation of the colour distracters, while keeping their luminance equal to the background (see Materials and methods). For both the orientation discrimination and the colour discrimination tasks, the main effects of quadrant and of distracter saturation were highly significant, as was the interaction between the two factors, and this was true for both M1 and M2 (entries 16–18, 21–23). As in the previous experiments with luminance distracters, the interactions followed from the fact that increases in distracter intensity led to strong

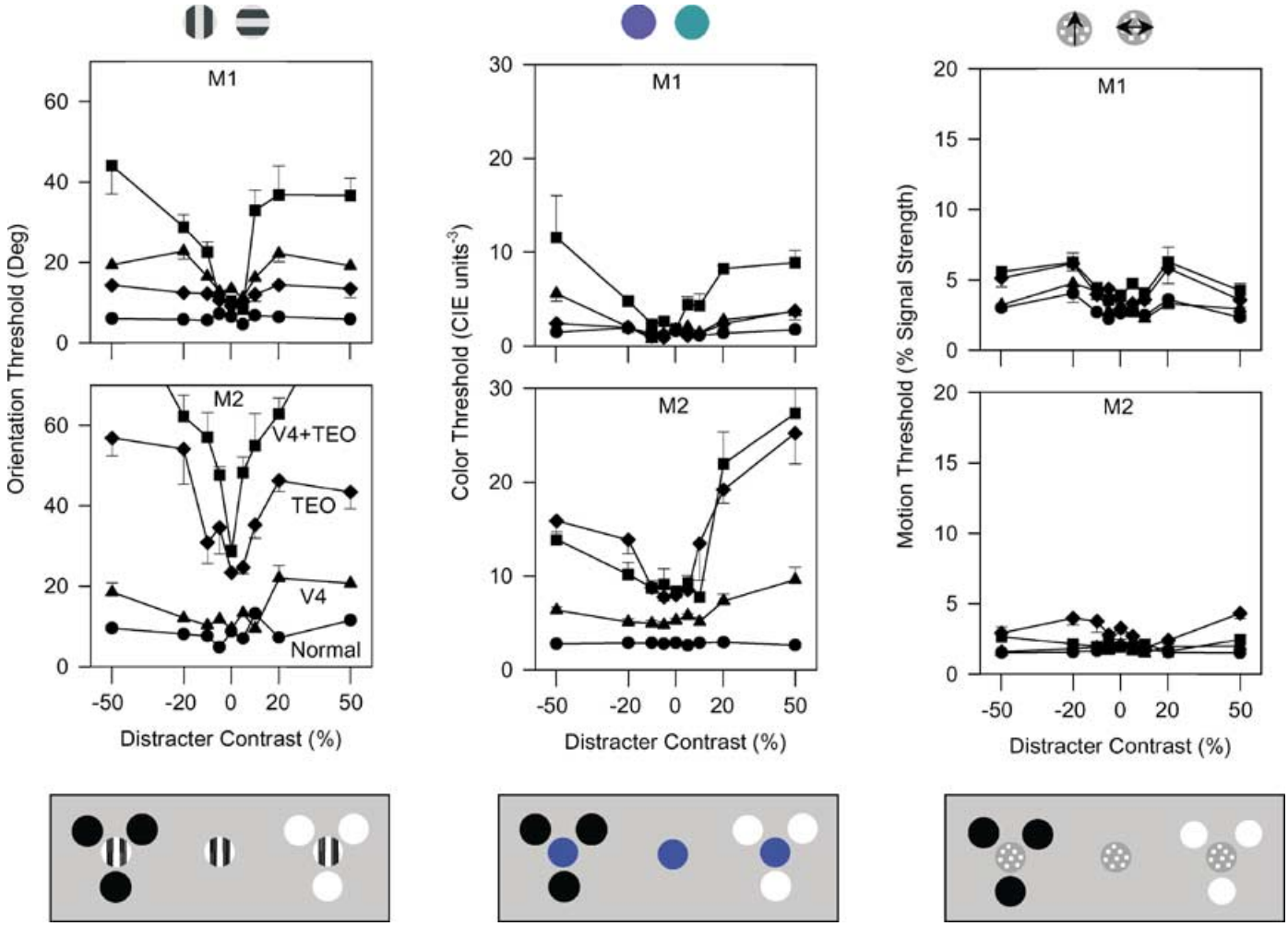

FIG. 3. Effects of luminance distracters upon the discrimination of orientation (left panels), colour (middle panels) and motion (right panels) for monkey M1 (top panels) and monkey M2 (bottom panels). Insets on top show for each pair of stimuli the reference stimulus on the left ('go' stimulus) and a variable stimulus on the right ('no-go' stimulus). Insets at the bottom are cartoons that illustrate the distracter contrast manipulation. Some aspects of these cartoons are enhanced for purposes of illustration (e.g. pixel size in motion targets), and do not reflect actual appearance of stimuli during testing. Only extreme distracter contrasts are shown (black distracters at −50% contrast and white distracters at 50% contrast). Only one configuration of distracter positions is shown, but during testing the position of distracters varied from trial to trial (see Materials and methods). In each of the six panels, 84% correct thresholds are plotted as a function of distracter contrast, in the normal quadrant (dots), the V4-affected quadrant (triangles), TEO-affected quadrant (diamonds) and the V4 + TEO-affected quadrant (squares). Each data point represents the average of four–eight thresholds (average n close to 6) and error bars represent standard errors. Absence of error bars indicates that standard errors were smaller than symbol size. For details on tasks and threshold measurements, see Materials and methods. The data with grating target and luminance distracters were reported before (see fig. 2 in De Weerd *et al*., 1999).

impairments of orientation and colour discriminations in lesion-affected quadrants, while in the normal quadrant, colour distracters did not increase either orientation or colour thresholds. Specifically, linear contrasts applied to orientation thresholds in the normal quadrant showed no significant effects of colour distracters in M1 (entry 19), and a small but significant decrease of orientation thresholds in M2 (entry 20). Likewise, colour thresholds determined in the normal quadrant of either monkey showed no significant effects of colour distracters (entry 24). Note that orientation and colour thresholds in TEO-affected and V4 + TEO-affected quadrants were greater in M2 than in M1.

In the motion discrimination task with colour distracters, there were no significant main effects of quadrant or distracter saturation in M1, and no significant interaction between these two factors (entries 25–27). In M2, there was a significant main effect of quadrant (entry 25) and, although there was no significant effect of distracter saturation (entry 26), there was a small but significant interaction between distracter saturation and quadrant (entry 27). This interaction was caused by a small threshold increase at the highest distracter saturation in the TEO-affected quadrant (entry 28) (compared with the 40% saturation), combined with small but statistically significant threshold decreases in the V4 + TEO-affected (entry 29) and normal quadrants (entry 30). Although there was a hint of an effect of colour distracters in the TEO-affected quadrant in M2, overall we found little evidence that colour distracters increased the magnitude of motion discrimination thresholds.

Effects of motion distracters on orientation, colour and motion discrimination

Figure 5 shows the findings with motion distracters, whose strength was increased by increasing the local luminance contrast of the moving pixels, while keeping global luminance equal to the background (see Materials and methods). For all three tasks, we found significant main effects of quadrant, of distracter strength, and a significant interaction

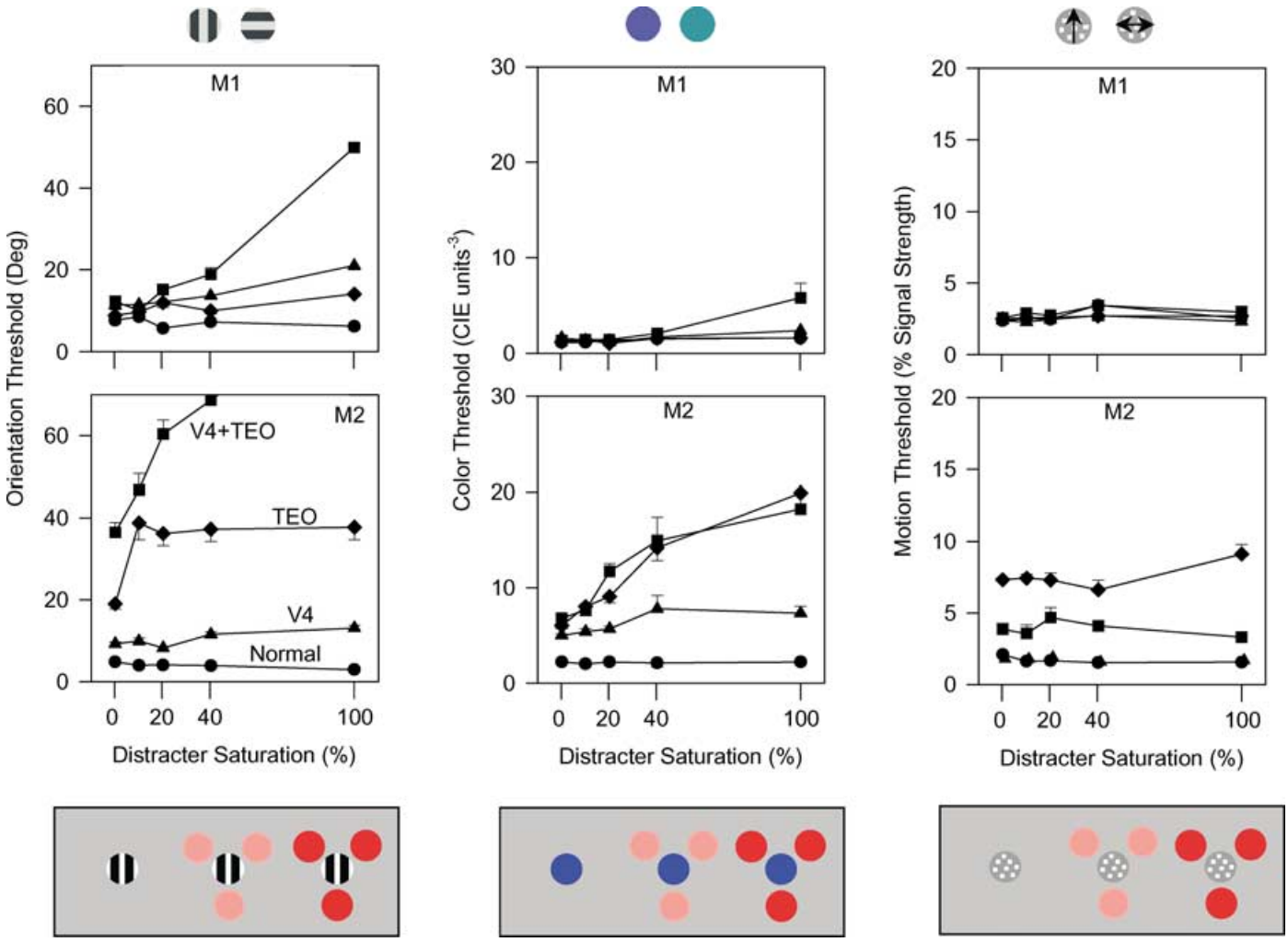

FIG. 4. Effects of colour distracters upon the discrimination of orientation (left panels), colour (middle panels) and motion (right panels) for monkey M1 (top panels) and monkey M2 (bottom panels). Insets on top show for each pair of stimuli the 'go' stimulus on the left and a 'no-go' stimulus on the right. The strength of the red distracters was manipulated by increasing colour saturation from zero (no distracters) to maximum (100%). Insets at the bottom symbolize displays with colour saturations of 0%, 40% and 100%. All colour stimuli were equiluminant with the background. Stimuli in the insets are illustrations that approach the appearance of stimuli shown during the experiments, although some aspects of the stimuli are enhanced for illustrative purposes (pixel size in motion targets). In each of the six panels, 84% correct thresholds are plotted as a function of distracter saturation, in the normal quadrant (dots), the V4-affected quadrant (triangles), TEO-affected quadrant (diamonds) and the V4 + TEO-affected quadrant (squares). Note overlap of dots and triangles in bottom, right-hand panel. Each data point represents the average of four–eight thresholds (average n close to 6) and error bars represent standard errors. For details on tasks and threshold measurements, see Materials and methods.

between the two factors for both monkeys (entries 31–33, 35–37, 39–41). Hence, motion distracters were the only ones to interfere with the discrimination of motion targets in lesion-affected quadrants and, thus, they were the only ones to reveal deficits for all three target types. Linear contrasts between thresholds with and without distracters indicated that motion distracters had no effect on thresholds in the normal quadrant in any of the tasks (entries 34, 38, 42), with the exception of the motion discrimination thresholds in M1's normal quadrant, which increased slightly as a function of the strength of the motion distracters (entry 42). Note that the motion thresholds in TEO-affected and V4 + TEO-affected quadrants were more elevated in M2 compared with M1.

Although the average luminance of all motion distracters equalled that of the background, the strength of the motion distracters was increased by increasing pixel contrast, and it could be argued that their effect was due to increases in local luminance contrast at the pixels' edges, rather than increases in the strength of distracting motion. However, because motion thresholds were unaffected by luminance disk distracters, even at their highest contrast against the background, it is unlikely that the mere presence of static, luminance-defined pixel edges around motion targets was sufficient to disrupt motion discrimination. Instead, the effects of motion distracters on motion targets likely were related to their dynamic nature.

Generalized interactions between targets and distracters

The principal question that motivated this study – the generality of distracter-induced impairments after lesions of V4 and TEO – is addressed by the combined data in Figs 3–5. In seven out of the nine experiments described, we found a significant interaction between visual field quadrant and distracter strength in both monkeys, caused by the large distracter-induced deficits in target discrimination in the V4 + TEO-affected quadrant, the smaller deficits in quadrants affected by a single lesion, and the absence of such deficits in the normal quadrant (Table 2). Thus, the principal results in all nine experiments were highly similar in both monkeys, and they suggest that lesions in V4 and TEO caused a broad pattern of interactions between targets and

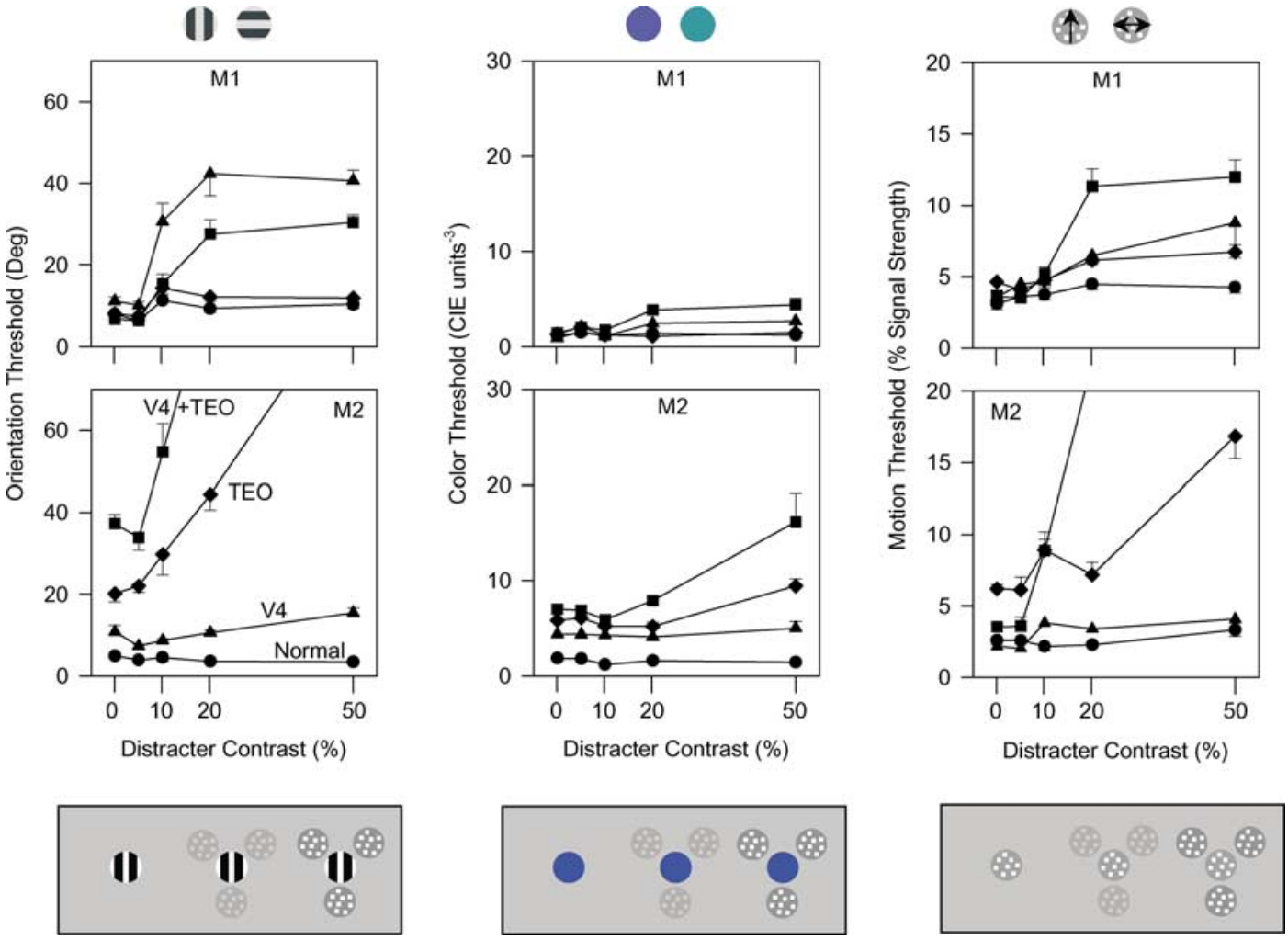

FIG. 5. Effects of motion distracters upon the discrimination of orientation (left panels), colour (middle panels) and motion (right panels) for monkey M1 (top panels) and monkey M2 (bottom panels). Insets on top show for each pair of stimuli the 'go' stimulus on the left and a 'no-go' stimulus on the right. We manipulated the strength of the distracters by decreasing the luminance of black pixels relative to the background, and increasing the luminance of white pixels relative to the background. This led to enhanced local contrast within the distracters, but the average luminance of the distracter was kept equal to the background in the stimuli used during experiments. Insets at the bottom are cartoons that symbolize displays with distracter contrasts of 0%, 20% and 50%. Stimuli in the insets approach the appearance of stimuli shown during the experiments, but some aspects of the stimuli are enhanced for illustrative purposes (pixel size in motion targets and motion distracters). In each of the six panels, 84% correct thresholds (quantified as percentage signal dots) are plotted as a function of distracter saturation, in the normal quadrant (dots), the V4-affected quadrant (triangles), TEO-affected quadrant (diamonds) and the V4 + TEO-affected quadrant (squares). Each data point represents the average of four–eight thresholds (average n close to 6) and error bars represent standard errors. For details on tasks and threshold measurements, see Materials and methods.

distracters defined in multiple feature domains. These data indicate that V4 and TEO are a neural substrate for selective attention mechanisms that apply to a broad range of stimuli.

Despite the impressive similarity of the results from the two monkeys, a few differences between the monkeys are noteworthy. Beyond the finding that thresholds in the TEO-affected and V4 + TEO-affected quadrants were generally larger in M2 than in M1, the most striking difference between the two monkeys may be the larger effect of colour distracters on the discrimination of orientation and colour targets in M2, compared with M1 (Fig. 4). Furthermore, the effects of motion distracters on grating orientation thresholds in M1 was greater in the V4-affected quadrant than in the two other lesion-affected quadrants, whereas the opposite was true in M2 (compare triangles in left lower and upper panels in Fig. 5). We also observed the gradual appearance of a small deficit in motion discrimination in the absence of distracters in M2 (compare data in right-hand lower panel in Fig. 3, collected first, with corresponding data in Figs 4 and 5).

Quantification of distracter-induced lesion deficits

To compare the effects of distracters across the different targets and distracters statistically, we computed an attention deficit index (ADI). The ADI is the logarithm of the ratio between thresholds obtained with and without distracters, computed separately in each lesion-affected quadrant. This ADI is corrected for distracter-induced threshold increases in the normal quadrant (see Materials and methods). To perform statistical analysis of the ADIs, we expressed all distracter strengths for each distracter type as a percentage of maximum strength. This yields relative distracter strengths of 10, 20, 40 and 100 for all distracter types. Thus, we have made the assumption that these relative strengths were similar across different distracter types. This assumption seems reasonable because for each distracter type, the maximal strength was at saturation level and because the weaker distracter strengths had been chosen to represent equal relative distances from saturation level (see Materials and methods). Below, we will discuss

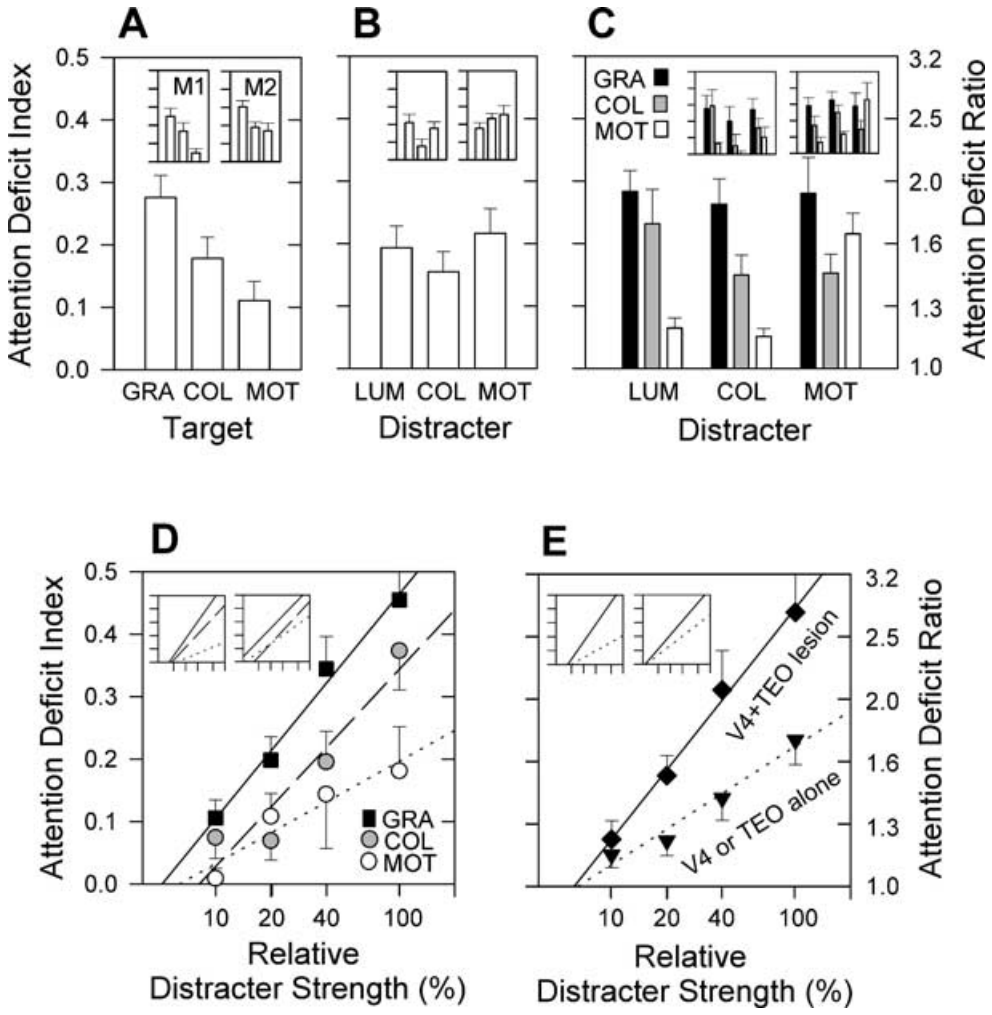

FIG. 6. Summary of attention effects after pooling of data from both monkeys. In each panel, lesion deficits are quantified as attention deficit indices (ADIs) on the left ordinate (see Materials and methods), and as corresponding attention deficit ratios on the right ordinate. The attention deficit ratio is the inverse logarithm of the ADI, and can be considered as the ratio between thresholds with distracters and thresholds without distracters within a lesion-affected quadrant (see Materials and methods). (A) to (E) show, respectively, the main effects of target (A) and distracter (B) on the ADI, the interaction between target and distracter (C), the interaction between relative distracter strength and target (D), and the interaction between relative distracter strength and lesion size (E). Relative distracter strength refers to the strength of distracters expressed as a percentage of maximum distracter strength (see Materials and methods), and is shown on a log scale in D and E. Black, grey and white symbols in C and D refer to grating, colour and motion targets, respectively. Squares in E refer to data from the V4 + TEO-affected quadrant, and triangles refer to pooled data from quadrants affected by a single lesion. In D, linear fits are described by $y = -0.082 + 0.164x$ for motion targets ($r^2 = 0.899$), by $y = -0.193 + 0.312x$ for colour targets ($r^2 = 0.895$) and by $y = -0.147 + 0.356x$ for grating targets ($r^2 = 0.988$). In E, linear fits are described by $y = -0.098 + 0.190x$ for data in quadrants affected by V4 or TEO alone ($r^2 = 0.963$) and by $y = -0.184 + 0.370x$ for the V4 + TEO-affected quadrant ($r^2 = 0.995$). Insets in each main panel show corresponding data separately in M1 (left) and M2 (right) using the same axes and conventions as used in the main panel. Error bars represent standard errors. COL, colour; GRA, grating; LUM, luminance; MOT, motion.

the common trends across monkeys first, after which some differences will be pointed out.

Common trends between monkeys. The ADI was calculated for all relative distracter strengths and lesion-affected quadrants for each of the nine combinations of distracter type and target type (see Figs 3–5). The ADIs were calculated separately in each monkey, based on the average thresholds shown in Figs 3–5. The ADIs obtained for V4 and TEO-affected quadrants were averaged in each monkey, to obtain an overall estimate of deficits in quadrants affected by a single lesion. With luminance distracters, ADIs for bright and dark distracters with corresponding absolute contrast values were averaged as well.

An ANOVA was carried out on the ADIs pooled over the two monkeys, with target type (3 levels), distracter type (3), relative distracter strength (4) and lesion size (2) as the different factors. We found significant main effects for target type (Fig. 6A) and lesion size (single area vs. combined lesions, see Fig. 6E), but not for distracter type (Fig. 6B, entries 43–46). Three two-way interactions reached significance as well. There was a significant interaction between distracter and target type (Fig. 6C, entry 47), between relative distracter strength and target type (Fig. 6D, entry 48), and between relative distracter strength and lesion size (Fig. 6E, entry 49). None of the other interactions reached significance.

There was a strong effect of target type on performance, and all three pair-wise differences between target types were significant (entries 50–52). Thus, on average, the discrimination of grating targets was most easily disrupted by distracters in the lesion-affected quadrants, whereas discrimination of motion targets was most resistant to the effects of distracters, with an intermediate effect of distracters for colour targets (Fig. 6A). This clear main effect of target type contrasts

with the absence of a significant main effect for distracter type (Fig. 6B).

The interaction between distracter and target types reflects the differential effects of the different distracter types on target discrimination thresholds (Fig. 6C). In particular, the discrimination deficits induced by luminance and colour distracters were much larger for grating and colour targets (black and grey bars in Fig. 6C) than for motion targets (white bars in Fig. 6C, entries 53, 54). At the same time, the discrimination deficits induced by motion distracters in the motion discrimination task matched the average deficit for grating and colour targets (entry 55).

The significant interaction between target type and the relative distracter strength suggests that increasing the distracter strength had different effects on the different target types. As shown in Fig. 6D, increases in relative distracter strength caused steeper increases in discrimination deficits for grating and colour targets than for the motion target. The smaller effect of relative distracter strength on motion targets, however, only reflects the fact that motion discrimination was unaffected by two of the three distracter types (entries 15, 27–30). When the data obtained with the motion target were excluded from ANOVA, there was no interaction between relative distracter strength and target (entry 56). More interestingly, the data in Fig. 6D corroborate the finding that the discrimination of grating orientation was most easily disrupted by distracters (see Fig. 6A). Indeed, Fig. 6D shows that this finding held even for the weakest distracter strengths (entries 57, 58). The effects of relative distracter strength on the ADIs (with relative distracter strength plotted on a log scale in Fig. 6D) were well fitted by linear regressions (see legend to Fig. 6D).

The significant interaction between relative distracter strength and lesion type indicates that increasing distracter strength had different effects in quadrants affected by a single or a double lesion. As shown in Fig. 6E, increases in relative distracter strength caused steeper increases in discrimination deficits in the V4 + TEO-affected quadrants than in quadrants affected by a V4 or a TEO lesion alone. Again, the data were well fitted by linear regression, and the slope of the regression in the V4 + TEO-affected quadrant was twice that of the regression obtained for quadrants affected by a single lesion (see legend to Fig. 6E).

Significant trends in the pooled data shown in Fig. 6 were generally observed in both monkeys individually (see insets in Fig. 6A–E). This was confirmed by additional analyses, in which the monkey was introduced as an additional factor (see legend to Table 2). This analysis showed that the main effect for target type (Fig. 6A), as well as the interactions between target and distracter types (Fig. 6C), between target type and relative distracter strength (Fig. 6D), and between relative distracter strength and lesion size (Fig. 6E) were not significantly different in the two monkeys (entries 59–62). By contrast, the effect of distracter type (Fig. 6B), which was not significant in the pooled data, was significantly different in the two monkeys (entries 63–66). This was due to the much larger effect of motion distracters (entry 66) and, especially, colour distracters (entry 65) in M2 compared with M1 (see below, and Fig. 6B and C insets).

Differences between monkeys. An inspection of Figs 3–5 shows that the differences between monkeys were primarily due to differential effects of distracters in the TEO-affected hemifield (comprised of TEO-affected and V4 + TEO-affected quadrants). An ANOVA in which the data for each lesion-affected quadrant were analysed separately, revealed a large interaction between the factors monkey and lesion (entry 67). Averaged over all target and distracter conditions, distracter-induced threshold elevations in the TEO-affected hemifield were larger in M2 (ADI of 0.25) than in M1 (ADI of 0.14), while in the V4-affected quadrants, threshold elevations were indistinguishable (ADIs of 0.10 and 0.11 in M1 and M2, respectively). This analysis also indicated that the larger effect of colour distracters and motion distracters in M2 compared with M1 (Fig. 6B insets) stemmed predominantly from the results in the TEO-affected hemifield, and less from differences between monkeys in the V4 quadrant. The larger impairments in the TEO-affected hemifield in M2 are consistent with the larger size of the TEO lesion in this animal.

Effects of chronology of testing. The presence of clear common trends in the data despite differences between monkeys in the timing of postoperative experiments (Table 1) suggests that those common trends are robust. However, we considered that some statistical effects might be due to interactions between recovery and the timing of experiments. In particular, we wondered whether recovery could have contributed to the finding that grating targets were significantly more affected by distracters than other target types (Fig. 6A). The data from monkey M1 shown in Figs 3–5 and summarized in Fig. 6, however, were collected in a time period (from Jul 1995 to Jun 1996) in which repeated measurements of the effects of luminance distracters on grating orientation discrimination revealed no evidence for recovery (Fig. 9). Although other target–distracter combinations were not retested, this suggests that M1's data in Figs 3–5 were collected during a period of stable postoperative performance. The data from monkey M2 shown in Figs 3–5 were collected in a period (from Dec 1996 to Jan 1997) in which there was some evidence for improvement in grating discrimination thresholds (see Fig. 9). However, apart from the initial measurement with grating targets, postoperative measurements with the different targets were carried out within a short time period for each distracter type (Table 1). Thus, as in the other monkey, it is unlikely that the greater vulnerability of grating targets to the effects of distracters in lesion-affected quadrants could simply reflect differential effects of recovery for different target types. Furthermore, because all measurements with luminance distracters were carried out first, followed by measurements with colour and motion distracters (Table 1), a main effect for distracter type should have been present if recovery had been a major factor (with the largest ADIs for luminance distracters, and smaller ADIs for colour and motion distracters). However, Fig. 6B shows that there is no main effect of distracter type.

Relationship between target-alone and distracter-induced impairments. Although the monkeys generally performed much worse with distracters than in the target-alone conditions in the lesion-affected quadrants, there were nonetheless some threshold elevations in the target-alone condition for some tasks (especially in M2). To test whether this increase in target-alone thresholds might be related in some way to the pattern of distracter effects, we first examined the impairments in the target-alone condition for orientation, colour and motion thresholds, pooled over all experiments shown in Figs 3–5. In M1, orientation thresholds for the target alone in the V4-affected and V4 + TEO-affected quadrants were slightly but significantly larger than in the normal quadrant (entries 68–71), although there was no such difference for colour (entry 72) or motion thresholds (entry 76). In M2, thresholds for the target alone in all lesion-affected quadrants exceeded thresholds measured in the normal quadrant for all three targets, except for the motion target in the V4-affected quadrant (entries 68–79). Thus, the lesions impaired performance with the target alone in one task in M1 (orientation discrimination) and in three tasks in M2, and those deficits were especially clear in the two quadrants affected by the TEO lesion. However, the pattern of discrimination deficits in the target-alone condition in the lesion-affected quadrants showed no clear relationship to the overall pattern of deficits

in the same tasks with distracters. For example, M1 showed no deficit in colour discrimination for the colour target alone, yet showed significant threshold increases when the colour target was shown with luminance, colour and motion distracters. Further, M1 showed no deficits for the motion target shown alone, yet showed significant threshold increases when the motion target was shown with motion distracters (but not by luminance and colour distracters). Conversely, M2 showed increased motion thresholds without distracters in the lesion-affected quadrants, yet showed no increase in thresholds when colour or luminance distracters were added to the display. Taken together, these data suggest that the pattern of results with distracters is not directly related to the pattern of deficits with the target alone.

Mechanisms of target–distracter interactions in lesion-affected quadrants

In the tasks described so far, the targets and distracters were all disks of the same shape and size. This similarity raised the possibility that the animals might have been capable of attending selectively to the target and filtering out distracters, but that the lesions caused the targets and distracters to form a stronger perceptual group (e.g. a single group of disk-shaped elements) than normal, making selective attention to the target more difficult (i.e. Gestalt grouping; see Koffka, 1935). If so, this grouping hypothesis would provide an alternative to the biased competition account. We reasoned that if this hypothesis were correct, then breaking up the groups by decreasing the similarity between the target and distracters should increase the accuracy of target discriminations in the lesion-affected quadrants.

We tested this idea by manipulating the size and shape of luminance distracters surrounding a grating target (Fig. 7), using three experimental conditions. In the first experimental condition, distracters were luminance disks with the same size and shape as the target grating (disk distracter condition). In the second experimental condition, we reduced grouping by using distracters with a different shape than the target (square distracter condition). In the third experimental

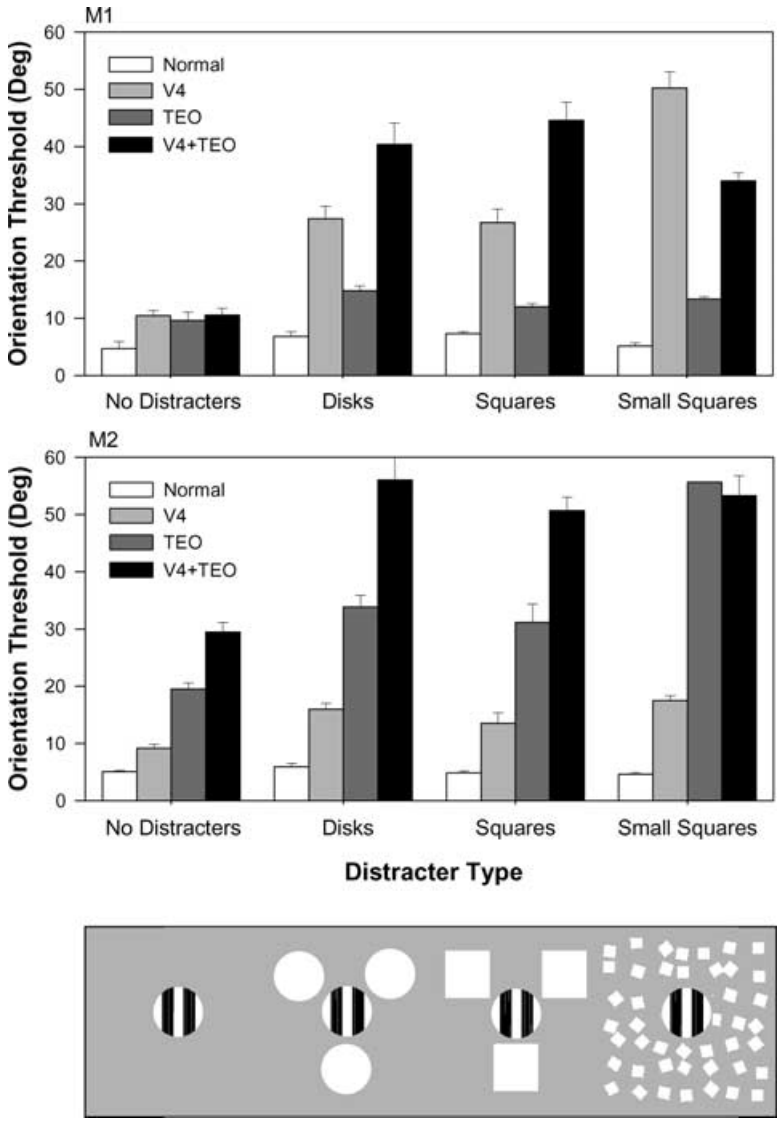

FIG. 7. Effect of similarity of target and distracter on grating orientation discrimination. The different target–distracter displays used are illustrated in the bottom panel. Thresholds (84% correct) in M1 (top) and in M2 (middle) obtained in the normal quadrant (open bars), V4-affected quadrant (light grey bars), TEO-affected quadrant (dark grey bars) and V4 + TEO-affected quadrant (black bars) were shown in the absence of distracters, in the presence of three circular luminance distracters, three square luminance distracters or a large number of small square distracters. Data points in M1 are based on six–eight observations in the no-distracter condition, and on 15–32 observations (19 on average) in the distracter conditions. Data points in M2 are based on 7–8 observations. Error bars represent standard errors.

condition, grouping was further reduced by decreasing the size of the square distracters, while increasing their number ($n = 44$) to keep total distracter area constant (small-squares distracter condition).

In the lesion-affected quadrants, all of the distracter types caused increased grating orientation thresholds compared with the thresholds measured with gratings shown alone, and this effect was weak or absent in the normal quadrant (entries 80–86). Importantly, in spite of the greater dissimilarity of the square distracters to the target, compared with the disk distracters, the thresholds in lesion-affected quadrants with the large square distracters (27.51° in M1 and 32.56° in M2, on average) were equivalent to the thresholds obtained with the three disk distracters (27.78° in M1 and 33.69° in M2) (entry 87). Furthermore, the thresholds with the even more dissimilar small square distracters (31.5° in M1 and 41.57° in M2) were actually larger than the thresholds obtained with the three disk distracters (entry 88). Hence, in both monkeys, reducing target–distracter similarity did not reduce the impairments caused by distracters in the lesion-affected quadrants, contrary to the hypothesis that excessive grouping, *per se*, of targets and distracters was responsible for the distracter-induced lesion impairments.

Another related, alternative hypothesis we considered was that the distracter-induced impairments were due to the greater complexity of the display with targets and distracters compared with displays showing the target alone. According to this hypothesis, the mere presence of multiple stimuli surrounding a target might have complicated visual analysis of the target, compared with displays in which the target was presented alone. By contrast, according to the biased competition hypothesis, the impairments were caused not so much by the presence of distracters but, rather, by the conflicting information provided by the distracters. Thus, because conflicting information from distracters was not filtered out in the lesion-affected quadrants, information about the target was 'blended' with information from the distracters in the responses of cells downstream from the lesion.

More specifically, according to biased competition theory, information in multiple stimuli becomes averaged with each other in the absence of selective attention, resulting in a signal not correlated with any of the stimuli, unless all stimuli carry the same information. Hence, this theory predicts that impairments should be greater in the case where the distracters carry information that conflicts with the target than in the case where distracters and target carry identical information. By contrast, the display complexity account predicts that there should be impairments in both conditions. These hypotheses were tested by comparing the effects of three distracters carrying orientation information conflicting with a grating target with the effects of three distracters carrying orientation information compatible with a grating target.

In the experimental condition with compatible distracters, a grating target was surrounded by grating distracters with orientations parallel to that of the target (parallel condition). In the experimental condition with conflicting distracters, the distracters' orientation was chosen randomly on each discrimination trial (random condition). We also remeasured grating orientation thresholds without distracters, and with the original luminance-defined disk distracters. In all of the distracter conditions, the target and distracters were arranged in a fixed, triangular formation, with the base of the triangle orientated towards the fixation point (Fig. 8). This arrangement was used to avoid the possibility that a threshold decrease in the parallel condition compared with the random condition might be due to the presentation of an informative grating stimulus close to fixation. These experiments were carried out in M1 only.

As in the previously described experiments, we found significant effects on orientation thresholds of quadrant tested and distracter

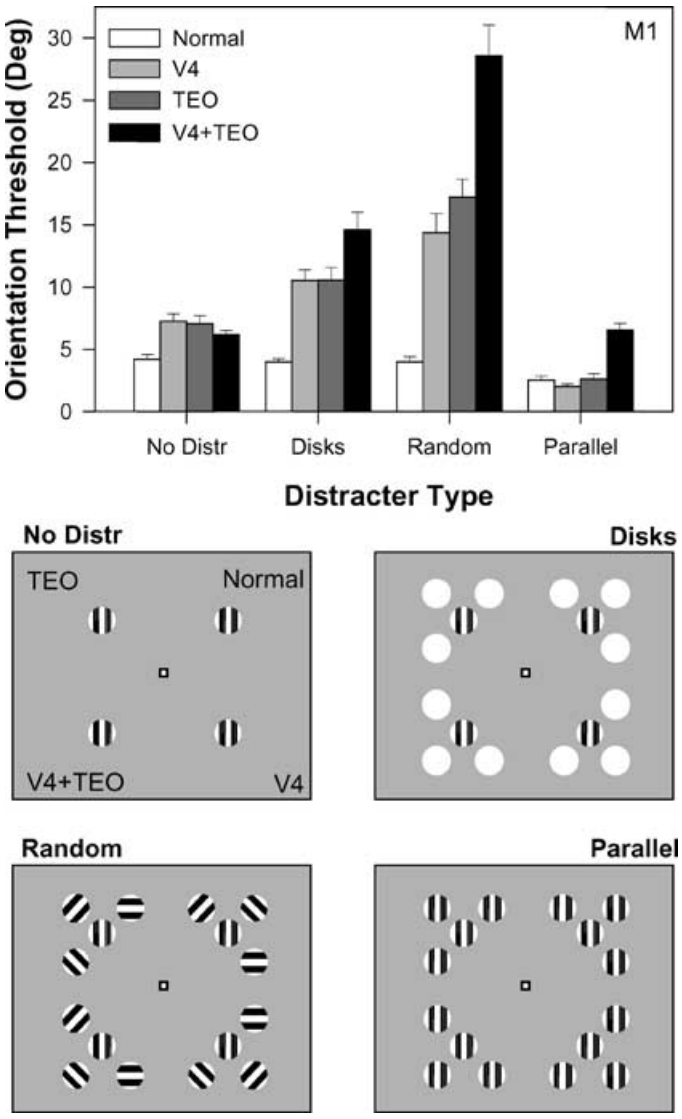

FIG. 8. Effects of grating distracters on orientation discrimination. Schematic illustration of the arrangement of the distracters is shown in the bottom panel in each quadrant, for different types of distracters (small central squares correspond to fixation point; drawings are approximately to scale). Target discriminations were carried out separately in individual quadrants. The arrangement of target and distracters in each quadrant was as shown in the bottom panel, and remained constant from trial to trial (see Materials and methods). Eccentricity of the target was 5.8°. The top panel shows orientation thresholds for monkey M1 in each quadrant in the absence of distracters (No Distr.), in the presence of luminance disk distracters (Disks), randomly orientated distracters (Random) and in the presence of distracters with an orientation parallel to that of the target (Parallel). Each data point is based on 12 threshold measurements. Other conventions as in Fig. 7.

condition, as well as a significant interaction between both factors (entries 89–91). Without distracters, there was a small but significant threshold increase in the lesion-affected quadrants compared with the normal quadrant (entry 92). The addition of luminance distracters significantly increased thresholds in the lesion-affected quadrants (entry 93), but not the normal quadrant (entry 94). In the lesion-affected quadrants, random distracters induced impairments beyond those seen with luminance distracters (entry 95), leaving target discriminations unaffected in the normal quadrant (entry 96).

By contrast, in the parallel (compatible) distracter condition, thresholds in the V4-affected quadrant and the TEO-affected quadrant with

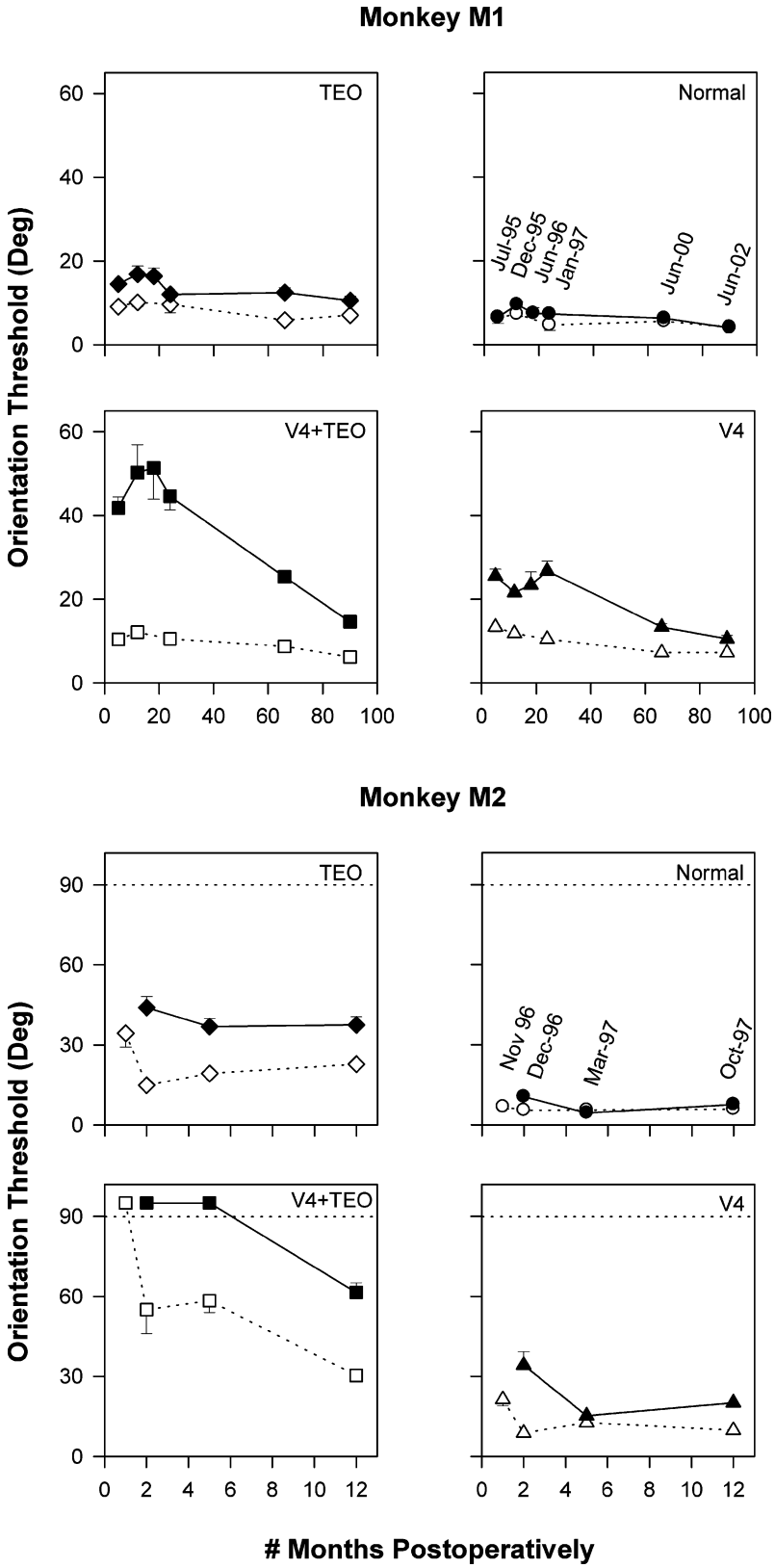

FIG. 9. Slow recovery of distracter-induced deficits during postoperative testing. The four panels for monkey M1 (top) and M2 (bottom) show grating orientation thresholds obtained in the absence (open symbols) and in the presence (solid symbols) of luminance distracters (three white disks). Thresholds are plotted as a function of the number of postoperative months elapsed since surgery, and the dates of data collection are indicated in panels displaying the thresholds in the normal quadrant. Grating contrast was 50%, except for monkey M1 in June 2000, when it was 67%. Distracter contrast was 50%. Each data point represents four–eight threshold measurements (average *n* close to 6), except two data points in M1, measured in June 2000 (10 observations in the *n* quadrant, and 16 in the lesion quadrants) and in June 2002 (12 measurements in all quadrants). The June 2002 data points in M1 were obtained with a fixed distracter configuration (see Fig. 8). All other data were obtained with a variable distracter configuration (see Materials and methods). Note the difference in abscissa between the two monkeys. Error bars represent standard errors.

TABLE 3. Performance in acuity and pattern discrimination tasks

	Acuity Test						Pattern Discrimination	
	SF = 1.9	SF = 2.6	SF = 4.0	SF = 5.2	SF = 7.8	SF = 15.6	+vs T	H vs U
M1, quadrant								
N	100 ± 0	–	99 ± 1	100 ± 0	–	99.5 ± 0.5	0.31 ± 0.04	0.32 ± 0.01
V4	100 ± 0	–	100 ± 0	100 ± 0	–	99.5 ± 0.5	0.81 ± 0.03	0.94 ± 0.01
TEO	100 ± 0	–	100 ± 0	100 ± 0	–	98 ± 2	0.44 ± 0.04	0.68 ± 0.03
V4+TEO	100 ± 0	–	100 ± 0	98.25 ± 1.75	–	98.5 ± 1.5	0.91 ± 0.02	0.93 ± 0.01
M2, quadrant								
N	–	100 ± 0	96.5 ± 2.36	98.25 ± 1.75	95.5 ± 1.66	91.57 ± 3.82	0.42 ± 0.02	–
V4	–	96.5 ± 2.02	100 ± 0	99 ± 1	93 ± 3.11	79.75 ± 2.86	0.74 ± 0.02	–
TEO	–	100 ± 0	100 ± 0	95.5 ± 1.66	92.25 ± 1.44	73.14 ± 3.5	>1 ± 0	–
V4+TEO	–	96.25 ± 1.43	98.25 ± 1.75	95.75 ± 2.53	93.75 ± 0.75	73.5 ± 2.53	>1 ± 0	–

Percentage correct performance (mean ± SEM) in the acuity task (see Materials and methods) is shown for various spatial frequencies (SF) in M1 and M2. Pattern discrimination thresholds (84% correct) are shown in the normal and lesion-affected quadrants for the '+ vs. T' discrimination task (M1 and M2) and the 'H vs. U' task (M1 only) (see Materials and methods for details). Each mean represents 8–10 data points in M1 and 3–5 in M2.

distracters were equal to thresholds in the normal quadrant with distracters (entries 97, 98), and significantly lower than thresholds obtained in the normal quadrant without distracters (entry 99). Thus, in the normal, V4-affected and TEO-affected quadrants, it appears that the compatible 'distracters' provided information that was useful to solve the discrimination task. In the V4 + TEO-affected quadrant, there was no difference between thresholds obtained in the parallel distracter condition and the condition without distracters (entry 100), and performance with compatible distracters was equivalent to performance with no distracters at all. These results are contrary to the display complexity hypothesis, but consistent with the biased competition account.

It should also be noted that the thresholds with luminance disk distracters (Fig. 8) were significantly lower than those reported in several previous experiments (e.g. see Fig. 7), carried out years earlier (Table 1). This improvement may well be related to recovery in the lesion-affected quadrants (Fig. 9), but the absence of the presumably most effective distracters (closest to the fovea), and the absence of trial-to-trial randomization of distracter positions (see Materials and methods) might have contributed as well.

Stability of distracter-induced deficits

Over years of postoperative testing, we found evidence for extremely slow and incomplete improvement of function in the lesion-affected quadrants. This is illustrated in Fig. 9, which plots the effect of luminance disk distracters on grating orientation thresholds in the normal and the lesion-affected quadrants over the course of several years. In the first 1–1.5 years following the lesions, there was no recovery in M1 but some recovery in M2, especially in the V4 + TEO-affected quadrant (note different time scales for the two monkeys in Fig. 9). In M1, which had the smaller lesion, an additional 5 years of postoperative testing resulted in significant but still incomplete recovery.

Assessment of other perceptual capabilities

To further evaluate perceptual impairments in the lesion-affected quadrants, we also tested acuity and pattern discrimination in the target-alone condition. Because the acuity task required the monkeys to discriminate gratings of high spatial frequency from a homogeneous grey region (matched in size and overall luminance; see Material and methods), aliasing might have led to an overestimate of acuity in both the normal and lesion-affected quadrants. However, the critical issue was the comparison of acuity in these quadrants (Table 3). We found no evidence for acuity deficits in M1, up to 15.6 c/° in the lesion-affected quadrants (entries 101–103). In M2, acuity was intact for gratings up to 7.8 c/°, but a significant impairment was found for the 15.6 c/° grating in all three lesion-affected quadrants (entries 101–106). These very limited effects of the lesions on acuity are in agreement with other studies in which basic visual capabilities were found to be intact after mid-level and high-level extrastriate lesions (e.g. Merigan, 1996; Huxlin & Merigan, 1998). In addition, a previous study with the same two monkeys (De Weerd *et al*., 1999) demonstrated that grating orientation discrimination was unimpaired in lesion-affected quadrants for contrasts as low as 2.5%. Hence, the data indicate that the distracter-induced discrimination deficits are unlikely to be due to low-level sensory impairments. This conclusion is also consistent with the fact that the presence or absence of target discrimination deficits in the target-alone condition did not predict distracter-induced threshold increases in lesion-affected quadrants (Figs 3–5).

Table 3 also shows results obtained in the '+ vs. T' discrimination task (see Materials and methods). Both monkeys showed large threshold increases in all three lesion-affected quadrants in this task (entries 107–110). M1 also performed a variant of the task, the 'H vs. U' discrimination task, and showed deficits similar to those seen in the '+ vs. T' discrimination task. A common aspect of these discriminations is that, except for the largest pattern difference, the variable stimulus and the standard stimulus both contained crossings of line segments. In order to perform the pattern discriminations successfully, these crossings, which are pop-out elements (Julesz & Bergen, 1981) and thus powerful distracters, had to be ignored. It is therefore possible that the deficits were related to an inability to ignore the crossings, which suggests that impairments of selective attention might contribute to these deficits. As in previous experiments, the effects of the TEO lesion were more severe in M2 compared with M1.

Discussion

The finding that distracters interfered with the discrimination of targets defined within several stimulus feature domains, and often across different stimulus domains, constitutes strong behavioural evidence for a broad role of V4 and TEO in the attentional filtering of distracting information. Several specific issues are discussed below.

What makes distracters distracting?

Human psychophysical studies of normal vision have demonstrated that target discriminations are impaired by the presence of distracters under conditions of limited attention (e.g. Theeuwes, 1991; Braun, 1994; Joseph *et al*., 1997; Caputo & Guerra, 1998; Zenger *et al*., 2000;

see also Pashler, 1988). This is consistent with the biased competition account of attention, in the sense that the loss or weakening of top-down attentional inputs to extrastriate neurons processing the target would result in the 'contamination' of target-related information with distracter-related information (Desimone & Duncan, 1995; Lee *et al*., 1999; Reynolds *et al*., 1999; Itti & Koch, 2000).

However, in the absence of top-down attentional biasing signals, coarse target discriminations often remain possible, raising the question of the extent to which information about the target features remains available during an 'unbiased' competition between target and distracters. Reynolds *et al*. (1999) showed that in the absence of attention, the response to multiple stimuli presented inside the RFs of V2 and V4 neurons can be described as a weighted average of the responses to the stimuli presented individually. Consistent with this, a recent psychophysical study in humans demonstrated that the signals from stimuli in crowded displays are averaged with each other (Parkes *et al*., 2001).

The present results suggest that signal averaging among targets and distracters may take place in the quadrants affected by lesions in V4 and TEO. Because RF sizes in V1 and V2 are too small to fully contain the stimulus displays in the present study, these areas probably did not play a major role in the 'filtering-out' of distracters (Moran & Desimone, 1985; De Weerd *et al*., 1999; Kastner & Ungerleider, 2000). Further, the lesions in V4 and TEO removed neurons that were well-suited to contribute to the attentional filtering of distracters, because their RFs would have encompassed both the target and distracters (Gattass *et al*., 1988; Boussaoud *et al*., 1991). Therefore, an 'unfiltered' signal from areas V1 and V2 must have been used for further perceptual analysis by downstream areas spared by the lesion and, under those conditions, neuronal responses in these downstream areas might reflect an averaging of signals derived from target and distracters.

Several of our findings shed light on how each stimulus' weight in the averaging process may be determined in lesion-affected quadrants. We found that the accuracy of target discriminations diminished with the strength of distracters (see also Schiller & Lee, 1991; Schiller, 1993; De Weerd *et al*., 1999). This suggests that the contribution of the target to the average response in a neural population diminished as a function of the magnitude of responses to the distracters. In other words, especially after the combined loss of V4 and TEO, the weight of each stimulus in the averaging process was determined predominantly by physical parameters of the stimuli rather than by their behavioural relevance.

Motion discriminations in the lesion-affected quadrants were resistant to influences from luminance and colour distracters, and were impaired by motion distracters only. This can be understood by incorporating a temporal component in the averaging process. The moving stimuli likely caused a more sustained neural response than the colour or luminance-defined stimuli. Therefore, motion distracters would have an increased contribution to the average neuronal signal relative to that of static targets. Likewise, the sustained signal from the motion targets would dominate the more transient signal from the static distracters, thereby sparing discrimination of motion targets surrounded by static distracters. The fact that motion distracters impaired the discrimination of motion targets suggests that neither had an advantage in the averaging process.

Grating distracters severely disrupted the discrimination of target gratings only if target and distracter orientations were conflicting, but not when the orientations in all stimuli were matching. This provides additional support for signal averaging. A related finding was that, except in the V4 + TEO-affected quadrant, the presence of parallel distracters decreased thresholds compared with the condition without distracters. This suggests that in the normal, V4-affected and TEO-affected quadrants, the monkey pooled the signal from several orientated stimuli in order to improve performance. By contrast, in the V4 + TEO-affected quadrant no such pooling took place. Hence, the removal of V4 and TEO neurons with RFs spanning the spatial range in which we presented the stimuli not only interfered with the elimination of information when it was distracting, it also interfered with the pooling of dispersed information when it was useful.

The discrimination of a target grating in the lesion-affected quadrants was more severely impaired by randomly orientated grating distracters than by luminance disk distracters, which could be due to several factors. First, in lower-order areas such as V1 and V2, grating stimuli are likely to drive neurons more effectively than luminance stimuli, which may render them less effective distracters. Second, the additional weight of randomly orientated grating distracters may also be related to extra-RF interactions in V1 and V2 among the grating stimuli (contextual effects). In an intact system, any contribution of such effects might be diminished by selective attention (Ito *et al*., 1998; Ito & Gilbert, 1999). Third, the orientation randomization of grating distracters is likely to introduce large trial-to-trial variability in the responses associated with any given orientation of the target grating (reducing signal-to-noise ratio), while luminance disk distracters are unlikely to induce such large variability.

Distracters, irrespective of their type, interfered more strongly with the discrimination of target gratings than with the discrimination of other target types. This finding may suggest that, in the ventral stream, the 'protection' of target contour information during the analysis of target objects, which results from the attentional filtering of distracters, is more important than the 'protection' of target colour or motion. This is in keeping with the role of the ventral stream in object recognition (see Desimone & Ungerleider, 1989), a capability which arguably requires greater precision in the perception of contours than in the perception of colour or motion.

We also found that monkey M2, whose TEO lesion encroached upon TE, showed comparatively larger effects of colour and motion distracters in the TEO-affected hemifield. This is in line with studies showing that colour perception (Heywood *et al*., 1988; Huxlin *et al*., 2000; Cowey *et al*., 2001) and the segregation of surfaces defined by motion (Britten *et al*., 1992; see also Sary *et al*., 1993) are impaired by lesions in the inferior temporal cortex.

The effect of motion distracters on motion discriminations and the absence of feature-specific distracter effects

The discrimination deficit observed with motion target and motion distracters was somewhat unexpected because the attentional modulation of competitive interactions between motion stimuli has been described within the RFs of MT neurons in the dorsal stream (Treue & Maunsell, 1996, 1999) but, so far, not in the ventral stream. This suggested that lesions of MT, but not of V4 and TEO, might affect a task in which a motion target must be selected from motion distracters. However, Treue & Maunsell (1996, 1999) investigated competitive interactions using stimuli that differed from those used in the present study. They used two objects (dots) moving in opposite directions inside the RF of MT cells, and found that attention to the target object strongly reduced the effect of the distracter on the cell's response. Groh *et al*. (1996), by contrast, used motion stimuli similar to ours while recording from MT cells, and did not find attentional modulation of the competition, which suggested that the attentional modulation of this type of motion stimulus might take place in ventral stream areas, as demonstrated in the present study. Thus, motion analysis in the dorsal and ventral stream areas may serve different purposes. Ventral stream areas may use motion for the purpose of figure-ground segregation (Britten *et al*., 1992; Sary *et al*., 1993; Marcar *et al*., 1995, 2000),

whereas dorsal stream areas such as MT may use motion for the purpose of analysing object motion, self-motion and optic flow (Dursteler & Wurtz, 1988; Tanaka *et al*., 1989; Lagae *et al*., 1994; Lappe *et al*., 1996).

The fact that V4 and TEO lesions impaired attention to motion-defined targets with motion distracters is consistent with the global nature of the attention deficits found in the present study and, in particular, with the absence of feature-specific attention deficits. This may be due, in part, to the fact that the different substrates in the ventral stream that process different stimulus features (orientation, colour, motion) are anatomically interconnected, and presumably interact (e.g. Desimone & Ungerleider, 1989; Lund *et al*., 1993; Merigan & Maunsell, 1993; Peterhans & von der Heydt, 1993; Levitt *et al*., 1994). Given these anatomical interconnections, a lesion in any ventral stream area may well affect the processing of multiple features.

Anatomical pathways supporting postoperative performance and recovery

The effect of distracters was twice as large in the quadrant affected by the combined lesion in V4 and TEO as in the quadrants affected by a single lesion. Hence, for the target and distracter displays used, which fit within the RFs of neurons in both V4 and TEO, one area compensated in part for the other. This may seem difficult to reconcile with the well-documented serial feed-forward connections in the ventral stream from V1 to V2, V2 to V4, V4 to TEO and TEO to TE (Desimone & Ungerleider, 1989; Distler *et al*., 1993). Nevertheless, some of these feedforward connections bypass single areas (Desimone *et al*., 1980; Nakamura *et al*., 1993), and this may permit one area to compensate for the loss of another. There is no evidence, however, for feedforward connections bypassing two areas, raising the possibility that in the V4 + TEO-affected quadrant, area TE could have been disconnected from lower order areas and thus deprived of visual input. If so, stimulus discriminations could have been mediated by areas posterior to area V4 or by areas in the dorsal stream, or else visual information was sent into area TE via other anatomical routes. In particular, visual information may have reached area TE from posterior areas either through the pulvinar (Webster *et al*., 1993) or through cortical areas in the superior temporal sulcus and parahippocampal gyrus (Martin-Elkins & Horel, 1992; Seltzer & Pandya, 1994; Suzuki & Amaral, 1994). Buffalo *et al*. (2000) confirmed in monkeys M1 and M2 that stimuli placed in the V4 + TEO-affected quadrant were effective in driving neurons in TE, although this activity was apparently insufficient to support normal attentional filtering of distracters. After several years, significant recovery occurred in M1, but not in M2. This suggests that area TE, and possibly parahippocampal area TF, contributed to recovery (both areas were partially damaged in M2, see Fig. 1).

Perceptual deficits measured without distracters

Perceptual deficits in simple target feature discrimination tasks tested without distracters were generally modest, although larger deficits were found in pattern discrimination. Furthermore, M2, whose TEO lesion partly involved TE, showed larger deficits in orientation and colour discrimination than M1 in the TEO-affected hemifield. These observations are in agreement with previous studies assessing effects of lesions of V4 (Wild *et al*., 1985; Heywood & Cowey, 1987; Schiller & Lee, 1991; Heywood *et al*., 1992; Walsh *et al*., 1992; Schiller, 1993; Walsh *et al*., 1993; Merigan, 1996), of TEO (Iwai & Mishkin, 1969; Iversen, 1973), of V4 and TEO combined (Cowey & Gross, 1970), and of TEO including TE (Dean, 1976, 1978; Iwai, 1985; Gaffan *et al*., 1986; Britten *et al*., 1992; Huxlin *et al*., 2000). The good discriminative abilities found in basic perceptual tasks make it unlikely that the pattern of results obtained with distracters could have resulted from a loss in basic visual capabilities (see Results).

Neural networks for attention, and the source of biasing signals

Neurophysiological (Moran & Desimone, 1985; Chelazzi *et al*., 1993, 1998; for review see Miller & Cohen, 2001) and anatomical (Webster *et al*., 1994) studies in monkeys suggest that the attentional biasing signals that modulate activity in extrastriate visual cortex may originate in prefrontal and posterior parietal areas. Similar attentional networks involving extrastriate and fronto-parietal cortex have been described in humans in imaging studies (e.g. Corbetta *et al*., 1995; Kastner *et al*., 1999; Hopfinger *et al*., 2000; for review see Parasuraman, 1998; Kastner & Ungerleider, 2000). Friedman-Hill *et al*. (2003) recently provided additional support for this idea by demonstrating that patient RM, who has a bilateral parietal lesion, was impaired on target–distracter tasks similar to the ones used in our monkeys. An assessment of a possible contribution of fronto-parietal cortex in the monkey to the selective attention tasks used in the present paper awaits further experimentation.

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Abbreviations

ADI, attention deficit index; RF, receptive field.

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