Brain (1993), **116**, 1337–1353

The characteristics of residual motion perception in the hemifield contralateral to lateral occipital lesions in humans

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SUMMARY

Unilateral damage to the lateral occipital region in humans can give rise to impaired motion perception in the contralateral visual field [Plant *et al.* (1993), *Brain*, **116**, 1303–1335]. We report the following characteristics of the residual vision. (i) Spatial acuity and spatial frequency discrimination are not affected. (ii) Contrast thresholds for direction-of-motion (DOM) discrimination of luminance modulated (LMod) sine-wave gratings is unaffected regardless of drift temporal frequency and the effect of spatial and temporal frequency on drifting/counterphase sensitivity ratios is normal (providing further evidence that cortical directionally selective mechanisms are intact). (iii) Contrast thresholds for DOM discrimination of contrast modulated (CMod) gratings are elevated by a log unit across a range of drift velocities. (iv) The residual motion perception shows neither a directional nor a naso-temporal asymmetry. (v) Weber fractions for velocity discrimination are shown in one patient in whom this measurement was carried out, to be elevated by around a factor of three but the functions relating velocity discrimination to stimulus contrast and to the velocity of the standard are parallel in the affected and unaffected hemifields. (vi) Weber fractions for temporal frequency discrimination using counterphase modulated gratings are also elevated.

We conclude that the degraded motion perception is mediated by mechanisms which have similar contrast and temporal properties to those subserving normal motion perception. Mechanisms subserving DOM discrimination of LMod gratings may be spared because they are more widely distributed in extra-striate cortex than mechanisms subserving non-Fourier (second-order) motion perception or velocity discrimination. The anomaly resembles that described in some recent animal studies of impaired motion perception after extra-striate cortical damage.

INTRODUCTION

It is known that damage to extra-striate visual cortex can give rise to selective impairment of visual motion perception in animals and humans but the magnitude of the deficit differs markedly in different studies. Permanent deficits in speed discrimination have been reported

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following lateral suprasylvian gyrus lesions in cats (Pasternak *et al.*, 1989) but in primates most workers have reported temporary deficits only (e.g. Newsome and Paré, 1988), although preliminary reports of a permanent deficit in speed discrimination have appeared (Merigan *et al.*, 1991; Vandenbussche *et al.*, 1991). None of these experiments has given rise to impairment of motion sensitivity which is as profound as that demonstrated by a 'motion-blind' patient (Zihl *et al.*, 1983; Hess *et al.*, 1989) who, it has been suggested, may have damage bilaterally to the homologue of V5 in the middle temperal area (V5-MT) and other related areas concerned with motion perception.

The disorder described by Zihl *et al.* (1983) occurs very rarely. Pötzl and Redlich (1911) described a patient with cortical blindness who was noted to be unable to perceive the movement of a light source in a dark room seeing instead 'several lights'. This patient exhibited a variety of other disturbances of visual function and the disturbance of motion perception could have been similar to that described by patients with abnormal visual persistence (*see*, for example, Kinsbourne and Warrington, 1963). She was, however, subsequently examined by Wertheimer (1912) who reported that she did not report seeing real or apparent motion, although she appreciated the colour of objects and perceived the motion of an acoustic impression as a 'fluttering back and forth'. Goldstein and Gelb (1918) described a patient who sustained a posterior bilateral penetrating injury and who, among other visual symptoms, reported impaired perception of movement. If a rapid movement of the arm was carried out in front of this patient he would say that the arm was at one moment up and at the next moment down, without an impression of movement occurring. With slower movements he would report seeing a succession of individual, isolated positions but not the simultaneous perception of several objects.

We considered that the study of cases with unilateral lesions may increase our understanding of the ways in which motion perception may be impaired following cerebral damage in humans because such examples may be more common than bilateral cases. In the accompanying article (Plant *et al.*, 1993) we have described three cases of lateral occipital damage giving rise to impaired motion perception in the contralateral visual field. The purpose of this further investigation has been to better define the characteristics of the visual deficit so that it can be discussed in the context of other human and animal studies of the effects of cerebral damage on visual motion perception. The abnormality reported in the accompanying article was demonstrated by measuring contrast thresholds for direction-of-motion (DOM) and speed discrimination tasks at intermediate temporal frequencies of modulation. In the experiments reported here we have obtained a more complete description of the residual vision. We have extended the observations to show that the findings are maintained across a wide range of both temporal frequency and contrast. We confirm that these patients are by no means 'motion-blind' (in the sense that cases of complete cerebral achromatopsia are 'colour-blind'). Residual motion perception is present and this has many normal characteristics: directionally tuned mechanisms are preserved; there is no directional bias; there is no naso-temporal asymmetry; and velocity discrimination is not differentially impaired at high or low temporal frequencies, or at high or low contrast levels.

METHODS

The clinical findings in Cases 1, 2 and 3 who participated in these additional investigations, the experimental apparatus and the majority of the methods employed have been described in the accompanying article (Plant

et al., 1993) In some of the additional experiments reported here Weber fractions for velocity discrimination ($\Delta V/V$) were measured rather than contrast thresholds. The gratings were drifted by changing the spatial phase of the grating at the start of each frame (or at the start of every *n*th frame where the spatial displacement per frame required was less than the width of each raster line). The smallest incremental unit possible was 1/1024 of a cycle per frame, equivalent to 0.09 Hz at the frame rate employed (100 Hz). In these experiments the spatial frequency was 0.5 cycles/degree and the stimulus duration was selected randomly by the computer from four preset values with a mean value of 400 ms (±20%) to minimize the possibility that the subject might use distance or duration cues (McKee 1981; Hess and Plant 1985). The drift velocity of the lower (standard) velocity was maintained at a constant value (16°/s except where otherwise stated) and the drift velocity of the higher (test) stimulus was incremented by an amount determined by the computer (ΔV). As the contrasts of the stimuli were not varied systematically in the staircase, they were randomly assigned one of four predetermined contrast levels within a narrow range (±20%) to reduce the possibility that the subjects could use changes in apparent contrast in the discrimination task. The contrast levels given in the Results are the means of these ranges.

In each trial of the staircase the standard and test stimuli were each randomly assigned to one of two successive intervals. The drift velocity of the standard grating did not vary between trials while the drift rate of the test grating did. Initially the test grating was a factor of two higher in drift velocity than the standard giving a value for $\Delta V/V$ of 100%. It was the subject's task to indicate by button presses in which interval the grating drifting at the higher rate had appeared. At each correct response $\Delta V/V$ was reduced by 20% until an incorrect response occurred when $\Delta V/V$ was increased by a factor of 2.5. The staircase continued until 40 trials had accumulated or at least six reversals had occurred. The mean of all the reversals except the first was then calculated. The direction of drift was usually varied randomly except in the experiments to determine whether or not there was a directional bias to the velocity deficit. In these experiments two separate staircases were randomly interleaved: in one the base velocity always drifted leftwards, and the test velocity always rightwards; in the other the converse was true. Because the two staircases were randomly interleaved it was not possible for the subject to identify the test velocity by its direction of drift, and the results of the two staircases were collected independently by the computer for analysis. No feedback was given to the subject in these experiments. A further difference in these experiments was that viewing was monocular (because we wished to compare performance in the nasal and temporal hemifields), whereas in all other experiments viewing was binocular. In some experiments Weber fractions for temporal frequency discrimination were measured using gratings modulated in counterphase. These experiments were in all respects otherwise identical to those in which drifting gratings were employed to measure velocity discrimination.

In order to determine how selective the effect is for motion perception a spatial frequency discrimination experiment was carried out in Case 1. The procedure was very similar to that employed to measure velocity discrimination, except that the base stimulus was a drifting sine-wave grating of 0.5 cycles/degree and the test stimulus was incremented in spatial frequency by an amount determined by the computer (DSF) and the subject's task was to determine which interval contained the grating of higher spatial frequency. Direction of drift and the initial phase of the gratings were randomly varied and the velocity and contrast were selected randomly from four predetermined values (maximum deviation 20% of the mean) to minimize the possibility that the subject might use changes in velocity or apparent contrast as cues to changes in spatial frequency. Each value of contrast or velocity quoted in the Results is the mean of one such range of values. In the same subject we also measured contrast sensitivity to gratings modulated in counterphase at 1 Hz at spatial frequencies ranging from 0.3 to 10 cycles/degree using the two-alternative forced-choice technique described in the accompanying article (Plant *et al.*, 1993). As in that article all the data shown are the means of at least three threshold measurements, each threshold being derived from a total of 40 trials.

RESULTS

Specificity of the effect for motion

In Cases 1 and 2 we were aware from the previous results that contrast sensitivity for gratings of 0.5 cycles/degree, contrast thresholds for an orientation discrimination task and Goldmann luminance and colour perimetry were not impaired at the visual field locations at which contrast thresholds for speed discrimination were abnormal. In Case 3 contrast sensitivity was impaired by a factor of about two in the contralateral upper

quadrant at the location tested. These observations were extended in Case 1 by measuring contrast sensitivity as a function of spatial frequency and spatial frequency discrimination as a function of temporal frequency. The results are shown in Figs 1 and 2. In Fig. 1

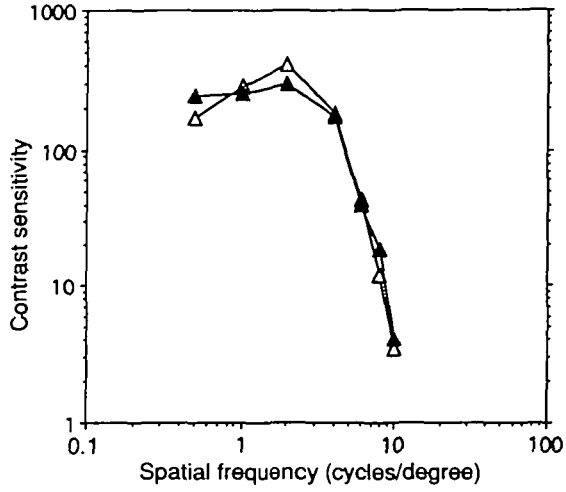

FIG. 1. In the previous study (Plant *et al.*, 1993) we demonstrated that contrast thresholds for low spatial frequency stimuli were not affected by the lesions in Cases 1 and 2. Here we show that contrast sensitivity (eccentricity = 10°) was not impaired in the contralateral field of Case 1 as a function of spatial frequency for stimuli modulated in counterphase at 1 Hz. Open triangles = ipsilateral; closed triangles = contralateral.

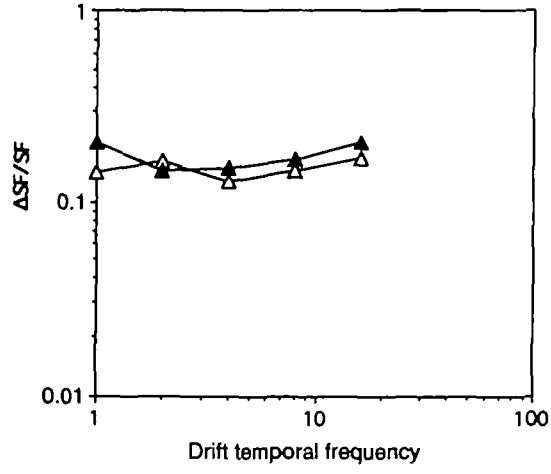

FIG. 2. Spatial frequency discrimination (contrast = 20%; eccentricity = 10° was measured in Case 1 for drifting sinusoidal gratings of 0.5 cycles/degree as a function of drift temporal frequency. Open triangles = ipsilateral; closed triangles = contralateral. There is no evidence for impaired spatial frequency discrimination in the contralateral hemifield where speed discrimination thresholds were elevated.

contrast sensitivity is plotted against spatial frequency and the results compared in the ipsilateral (open triangles) and contralateral (closed triangles) hemifields. The data are the means of at least three estimations of contrast sensitivity using the psychophysical procedure described in the accompanying article (Plant *et al.*, 1993). Although spatial acuity was not measured directly it can be seen from the similar shape of the high frequency limb of the contrast sensitivity functions shown in Fig. 1 that this was around 10 cycles/degree in each hemifield. Figure 2 shows that there was no evidence of impaired spatial frequency discrimination in the contralateral hemifield at drift temporal frequencies ranging from 1 to 20 Hz. Greenlee *et al.* (1990) have also found that, for a low spatial frequency, spatial frequency discrimination is unaffected by drift temporal frequency.

The effect of temporal frequency on the preserved thresholds for discrimination of DOM

The thresholds for DOM discrimination were unaffected in our cases. This observation is of particular interest as in the previously reported bilateral case of impaired motion perception (Hess *et al.*, 1989) direction discrimination was markedly impaired (e.g. contrast sensitivity for direction discrimination of a 1 cycle/degree grating drifting at 8 Hz was ~10, whilst the detection threshold for the same stimulus was ~100). In that report it was noted that the ability to discriminate DOM showed greater impairment at higher temporal frequencies of drift and for this reason contrast sensitivity functions for both detection and DOM discrimination were measured across temporal frequency in Cases 1 and 3. The results are shown in Fig. 3. As can be seen there was no increase in the discrimination : discrimination threshold ratio as a function of temporal frequency in the affected hemifield in either patient, although the overall reduction in contrast sensitivity in Case 3 for both tasks can be seen.

Drifting: counterphase sensitivity ratios in the affected and unaffected hemifields

Detection thresholds were measured for counterphase modulated and drifting gratings for three temporal frequencies (1, 4 and 16 Hz) and five spatial frequencies (0.5, 1, 2, 4 and 8 cycles/degree) in Case 1 in the contralateral hemifield at an eccentricity of 10°. Sensitivities were lower for drifting than for counterphase gratings under all conditions but the difference decreased at higher spatial and lower temporal frequencies. Thus at 1 Hz the drifting : counterphase sensitivity ratio was 1.47 at 0.5 cycles/degree falling to 1.16 at 8 cycles/degree. At 4 Hz the values were 1.6 and 1.21 and at 16 Hz 1.93 and 1.12 at 0.5 cycles/degree and 8 cycles/degree, respectively. Therefore the effect of spatial and temporal frequency on the drifting : counterphase ratio is normal (*see* Watson *et al.*, 1980; Pasternak, 1986).

The effect of velocity on the raised contrast threshold for DOM discrimination of a contrast modulated (CMod) grating

In the accompanying article (Plant *et al.*, 1993) we showed that the three patients in whom we found elevated thresholds for speed discrimination also showed elevated thresholds for DOM discrimination of a CMod grating drifting at 0.3 Hz (a velocity of 1.9°/s). We subsequently demonstrated, in Case 1 only, that the elevated threshold for DOM discrimination of the CMod grating was elevated by about a log unit across a wide range

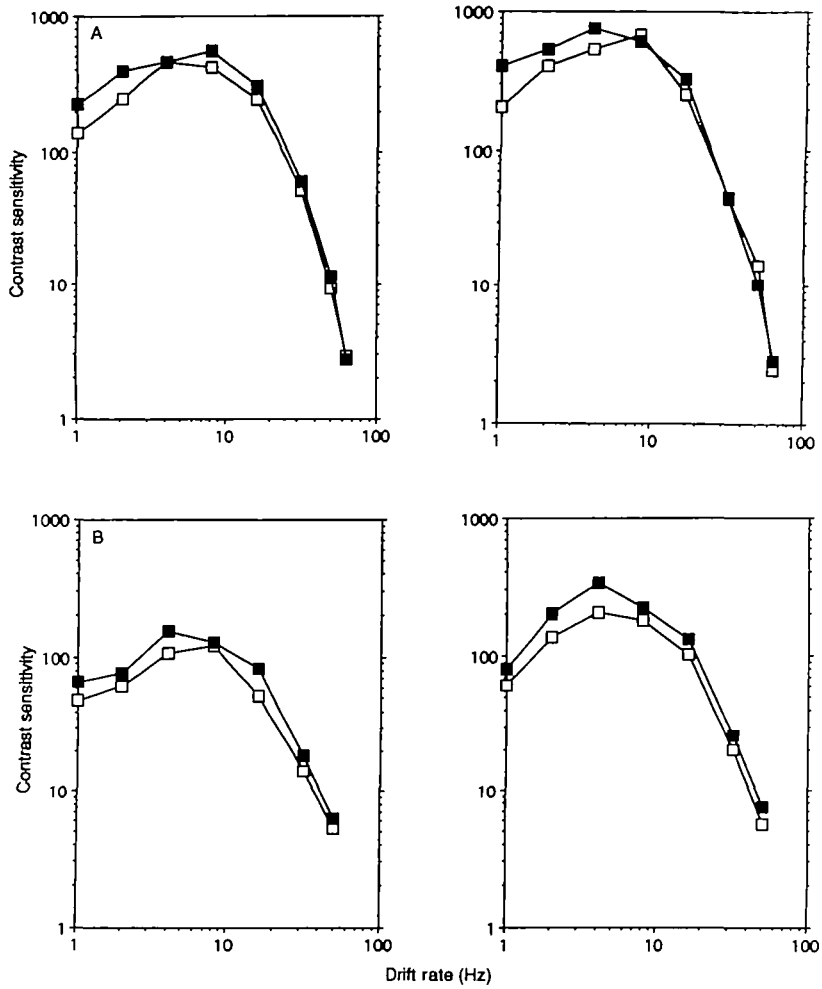

FIG. 3. A particularly important dissociation found in Cases 1, 2 and 3 was the preserved ability to discriminate the direction of drift of the sine-wave gratings as opposed to the contrast modulated grating. We wished to demonstrate that this was the case across temporal frequency (the other experiments were carried out at a drift rate of 8 Hz only). Here contrast sensitivity curves are shown for threshold detection (closed squares) and direction discrimination (open squares) of a 0.5 cycles/degree grating drifting at various temporal rates from 1 to 64 Hz. Results are shown for Cases 1 (A) and 3 (B) obtained in the upper quadrants of the visual field contralateral (on the left) and ipsilateral (on the right) to the lesion.

of stimulus drift velocities (Fig. 4; open and closed circles) while contrast detection thresholds for the complex waveform were comparable in the two hemifields (Fig. 4; open and closed triangles).

The distribution of the anomaly across the visual field

We also wished to know if the anomaly was distributed throughout the contralateral hemifield. In view of the field defect it was not possible to test the lower quadrant in Case 1, but at the same time as we obtained the results displayed in Fig. 6 of the

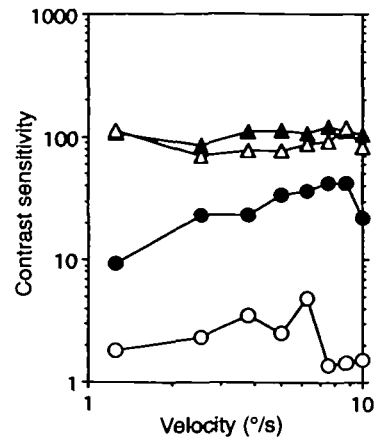

FIG. 4. Contrast sensitivity is plotted against drift velocity for two tasks (simple detection and DOM discrimination) and the results are compared in the ipsilateral and contralateral upper quadrants of the visual field in Case 1. The stimulus was an LMod sinusoidal grating of spatial frequency 0.5 cycles/degree the contrast of which was modulated in space by a sine wave of 0.08 cycles/degree (*see* Fig. 1 of the accompanying article, Plant *et al.*, 1993). Contrast thresholds for detecting the presence of the stimulus are similar in the two hemifields but the thresholds for DOM discrimination are elevated by around a log unit in the hemifield contralateral to the resection at all drift velocities tested. Triangles = detection; circles = direction; closed symbols = ipsilateral; open symbols = contralateral.

accompanying article (Plant *et al.*, 1993), we measured detection : speed discrimination sensitivity ratios for the 8 and 10 Hz pair at 10° and 30° eccentricity within the upper quadrants (such sensitivity ratios are plotted for a number of tasks in Fig. 7 of Plant *et al.*, 1993). In Fig. 5 it can be seen that the thresholds for the speed discrimination task are elevated to a comparable degree at these two locations in the upper quadrant. In Case 2 we carried out a similar exercise but, as that patient did not have a field defect following the resection, we were able to compare the anomaly in the upper and lower quadrants. We measured detection : direction discrimination ratios for the CMod grating (beat) stimulus. The results are shown in Fig. 5(B) where it can be seen that the ratio was elevated by a similar amount in both the upper and lower quadrants of the contralateral field.

Directionality and naso-temporal symmetry of the speed discrimination deficit

The purpose of this experiment was to explore the possibility that the deficit might differ in the nasal and temporal monocular fields and also the possibility that the anomaly may show a directional bias. Directional bias and monocular naso-temporal hemifield differences are known to occur in various human anomalies of motion perception or eye movement control, or both. Weber fractions for velocity discrimination were measured as described in Methods. However, instead of randomizing the direction of drift the base velocity was always presented in one direction and the test velocity in the opposite direction. Let us suppose that horizontal motion from temporal to nasal were reliably perceived as slower than horizontal motion from nasal to temporal. Then, in each eye, the Weber fractions should have been less (possibly achieving negative values) for nasalward than temporalward motion of the base velocity, as nasalward motion would be matched with a lower test

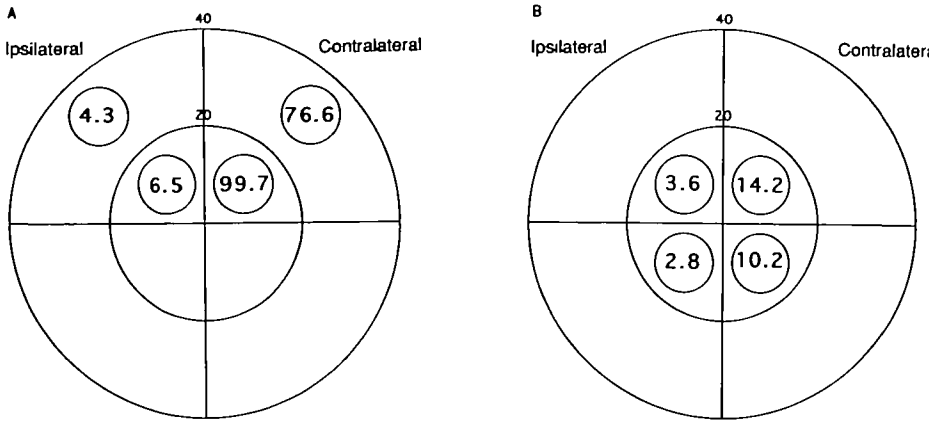

FIG. 5. In A, detection and speed discrimination ratios (sine wave = 8 and 10 Hz) are plotted at four locations in the upper quadrants of the binocular visual field of Case 1. Most of the tests on this patient were carried out at an eccentricity of 10°. Here it is shown that speed discrimination was also defective at an eccentricity of 30°. In B, detection/direction discrimination ratios are plotted for the contrast-modulated grating (beat). Most of the tests in this patient were carried out in the upper quadrant, here it is shown that the contrast threshold for direction discrimination of this stimulus is also elevated in the lower quadrant.

velocity. On the other hand, if leftward motion were perceived as drifting more slowly in each eye then a similar difference would have been observed for the leftward drifting base velocity for either eye. As a third possibility there may have been a selective impairment of velocity discrimination affecting the crossed or uncrossed contralateral hemifield, regardless of direction of drift, to explore this possibility testing was carried out monocularly.

As can be seen from the results plotted in Fig. 6, there was no evidence for a selective impairment of motion perception by field or direction. In all four conditions the Weber fractions in the affected hemifield are similar, and show a similar impairment relative to the unaffected hemifield in all three cases. The only exception to this was in Case 2 where the Weber fractions were lower for rightward drifting base velocities. Across the three subjects, however, there was no consistent pattern to suggest a directional bias or a naso-temporal asymmetry.

Velocity and temporal frequency discrimination across temporal frequency

The 'motion-blind' patient is known to have relative preservation of motion perception at low stimulus velocities (Zihl *et al.*, 1991) and it has been suggested that her residual motion perception may be mediated by early mechanisms (possibly V1 and V2). We had also observed in our Case 1 that contrast thresholds for speed discrimination improved during the weeks following the resection for a 4 and 8 Hz pair, but not for an 8 and 10 Hz pair. Furthermore, in Case 2 thresholds for the 4 and 8 Hz pair were not affected by the resection. We wished to know whether this indicated a temporal frequency (or velocity) specificity of the anomaly or if it simply reflects the ease or difficulty of the discrimination task (4 and 8 Hz represents a Weber fraction of 100% as opposed to 25% for the 8 and 10 Hz pair). Several months following the resection, Weber fractions for

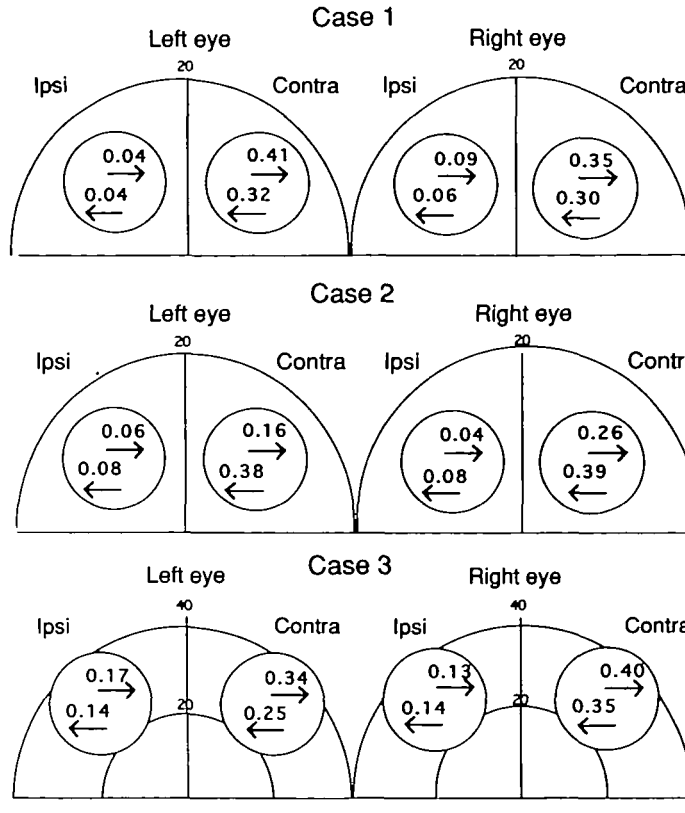

FIG. 6. We wished to determine whether there was any difference in the anomalous speed discrimination with respect to direction of horizontal motion of the stimulus or with respect to the stimulated monocular hemifield (nasal or temporal). Weber fractions for velocity ($\Delta V/V$) are shown for four locations in the upper monocular quadrants for Cases 1, 2 and 3 all of whom showed an elevation in Weber thresholds when tested binocularly in the upper quadrant contralateral to the lesion. The arrow indicates the direction of horizontal motion of the reference velocity (the test velocity always drifted in the opposite direction). There was no difference between the elevation of the Weber fraction comparing the performance in the contralateral nasal and temporal hemifields. There was no consistent difference with leftward or rightward motion of the reference velocity.

velocity discrimination were again measured in Case 1 (contemporaneous with the most recently obtained data points in Fig. 5 of the accompanying article). The purpose of these experiments was to determine whether the impaired velocity discrimination varied with temporal frequency. In Fig. 7 (closed symbols) the Weber fraction for velocity discrimination is plotted against the drift velocity of the base stimulus (at a mean stimulus contrast of 10%). The Weber fraction was found to be elevated by around a factor of three regardless of the base velocity.

The open symbols plot results obtained in an experiment to test whether the subject's ability to discriminate the temporal frequency of counterphase modulated gratings (as opposed to the velocity of drifting gratings) was also impaired. As can be seen, Weber fractions for temporal frequency discrimination (open squares) are higher than the Weber fractions for velocity discrimination in the ipsilateral hemifield (McKee *et al.*, 1986;

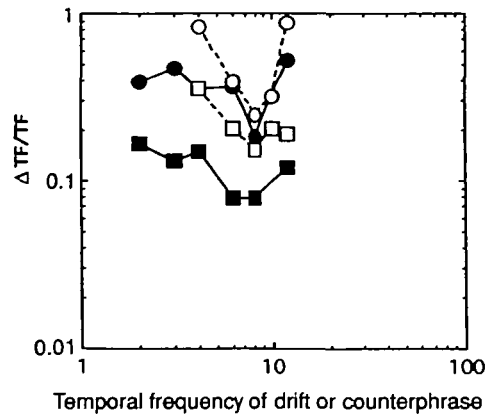

FIG. 7. For Case 1 only, the Weber fractions for velocity discrimination (closed symbols) and for temporal frequency discrimination (open symbols) are shown across a range of reference velocities (2–16 Hz or 4–32°/s) at a single contrast (10%), SF = 0.5 cycles/degree and eccentricity = 10°. Results are shown for each hemifield. Weber fractions for both stimuli are elevated in the contralateral hemifield and there is no marked effect of temporal frequency on the magnitude of the elevation. Squares = ipsilateral; circles = contralateral.

Pasternak, 1987) and it has certainly been affected by the resection (open circles). The improvement in velocity and temporal frequency discrimination at intermediate temporal frequencies is known to occur in normal vision (Thompson, 1984; Hess and Plant, 1985; McKee *et al.*, 1986; Plant, 1991*a*) and this feature is preserved in the affected hemifield.

Velocity discrimination as a function of stimulus contrast

It is known that at very low contrasts, Weber fractions for velocity and temporal frequency discrimination rise for human observers (Hess and Plant, 1985; McKee *et al.*, 1986). We wished to know whether the deficit in this patient could be considered to be equivalent to a reduction in stimulus contrast. The test used to demonstrate the deficit in the accompanying article (measuring contrast thresholds for velocity discrimination at a fixed Weber fraction) did not exclude this possibility. In Fig. 8 the Weber fraction for velocity discrimination of drifting gratings (at a base velocity of 16°/s) is plotted for Case 1 as a function of mean stimulus contrast. The fraction $\Delta V/V$ is elevated by a factor of approximately three regardless of stimulus contrast.

DISCUSSION

Other human studies: the perceptual deficit

The most extensively studied case of impaired motion perception has been the patient referred to as 'LM' (Zihl *et al.*, 1983, 1991). In addition to the fact that the cerebral damage was bilateral, the symptomatology in that case clearly represents a more profound impairment of motion perception than is described here. In terms of subjective reports our cases were not 'motion-blind' in the affected hemifield, they continued to appreciate the motion of objects in the visual field well. The only anomaly they report is that when the appearance of objects moving at the same speed is compared in the normal and affected

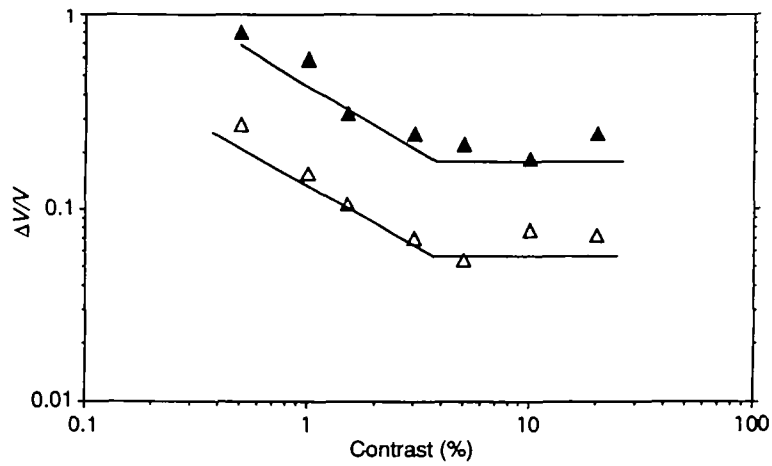

FIG. 8. For Case 1, the Weber fraction for velocity discrimination is plotted against stimulus contrast for each hemifield at a single reference velocity (8 Hz or 16°/s), SF = 0.5 cycles/degree and eccentricity = 10°. The fraction $\Delta V/V$ is elevated by the same amount across a wide range of stimulus contrast levels. Closed triangles = contralateral; open triangles = ipsilateral.

hemifields the perceived motion is slower in the affected hemifield. Our Case 1 has found this to cause errors in the exacting task of returning a racketball, but otherwise no gross functional deficit has occurred in any patient. This subjective report has not been quantified in our studies so far but it is interesting to note that the much more profound deficit of LM results in a reduced subjective velocity. Furthermore, the pursuit eye movement abnormalities reported by Newsome *et al.* (1985) in primates with lesions of V5-MT were compatible with an underestimation of target velocity.

Hess *et al.* (1989) reported that when viewing a drifting grating stimulus of 50% contrast LM was able to discriminate only 0 Hz from 0.1 Hz, 0.1 Hz from 1 Hz and 1 Hz from 6 Hz. A grating drifting at 6 Hz could not be discriminated from any higher temporal frequency (although such a discrimination at higher temporal frequencies was possible using counterphase modulated gratings). Our subjects were all capable of discriminating 8 and 10 Hz drift rates, albeit at an elevated contrast threshold, clearly LM would not be able to do this. Furthermore, LM showed significant impairment of DOM discrimination whether the stimulus employed was a sine-wave grating or drifting random dots. This can be compared directly with the results obtained in the present study because it was shown by Hess *et al.* (1989) that contrast thresholds for DOM discrimination of a 0.45 cycles/degree grating were elevated by one or two log units compared with a normal observer. Indeed this effect was particularly marked at 8 Hz (the drift rate used in the present study) and above 10 Hz LM was virtually unable to discriminate direction of drift at any contrast level. This supports the considerably milder nature of the perceptual deficit in our cases where the detection : DOM discrimination threshold ratio is unaffected. It may be that whilst striate cortex has been spared or largely spared in LM, outputs from striate cortex to extra-striate visual areas have been more extensively disrupted than in our three cases. Two other possibilities are that V5-MT and associated projections have been incompletely damaged in our cases or that the residual motion perception is

mediated by the ipsilateral hemisphere in our unilateral cases. Some recent studies in animals suggest that these explanations are less likely (*see below*). It is of course possible that the results obtained in our three cases do not represent the most severe impairment of motion perception in a hemifield that can occur. Further studies on larger numbers of patients with appropriately sited damage are required to pursue this question.

Vaina *et al.* (1990) have reported a case of bilateral parieto-occipital damage with impaired spatial localization and stereopsis. This patient also showed impaired performance on a speed discrimination task, but did not report the marked symptomatic perceptual difficulties experienced by LM. Vaina (1989) has reported impaired performance on a variety of motion tasks in patients with right, as opposed to left, posterior cerebral lesions. As free fixation was used in all the tasks, and some of the cases had hemianopia, such an effect must originate at a higher level in extra-striate visual cortex than lesions producing the anomaly decribed here. It so happens that our three positive cases had left hemisphere lesions but until more patients are tested we will not know whether there is any hemisphere asymmetry in the anomaly described in this paper.

The deficit in velocity and temporal frequency discrimination also differs from an anomaly of temporal frequency discrimination described in multiple sclerosis and optic neuritis (Plant and Hess, 1985; Plant, 1991*a*) where Weber fractions for temporal frequency discrimination were found to be elevated only at high base temporal frequencies and were associated with perceptual slowing of high flicker rates.

Comparison with animal studies

The consequences of ibotenic acid lesions of extra-striate visual area V5-MT have been studied in primates. Newsome *et al.* (1985) and Dürsteler *et al.* (1987) demonstrated impaired pursuit eye movements following such unilateral injections. Newsome and Paré (1988) found that following unilateral chemical lesions of V5-MT in rhesus monkeys there was an elevation in thresholds for the discrimination of DOM in a dynamic random dot display using masking motion noise as the variable. Siegel and Andersen (1986) (*see also* Andersen, 1989) demonstrated elevated thresholds for the detection of the onset of shearing motion and for the detection of form in a structure-from-motion task. Common to all these studies, however, was the transient nature of the effect, performance returning to normal or near normal several days following the injections.

In the one patient whom we have been able to follow over a considerable period following his surgery (Case 1) we noticed a marked and early improvement in contrast thresholds for the 4 and 8 Hz speed discrimination task (representing a Weber fraction of 100%) but not for the 8 and 10 Hz task (Weber fraction of 25%). The major anomaly has certainly persisted until several months following the resection. Permanent deficits in speed discrimination have, however, been demonstrated by Pasternak *et al.* (1989) in cats following bilateral ibotenic acid lesions of the lateral suprasylvian cortex, an area thought to be homologous to area V5-MT in primates. This latter study, despite the wider species gap, is of particular relevance to the present investigation because of the permanent nature of the deficit and also because similar tests to ours were employed to quantify the visual deficit. Pasternak *et al.* (1989) demonstrated that contrast thresholds for the discrimination of opposite DOM of drifting sinusoidal gratings were unaffected by these lesions and that the observed deficit was demonstrated only by measuring thresholds for discriminating differences in speed. Three cats were studied and under most conditions the Weber fractions

for speed discrimination were elevated following the lesions by a factor of about two at low contrasts (at higher contrast levels speed discrimination was largely unaffected, this feature is at variance with our findings, *see* Fig. 8). A preliminary report has appeared of similar results in macaque monkeys following bilateral ibotenic acid lesions of MT/MST where an elevated Weber fraction that is invariant with stimulus contrast and speed has been found (Merigan *et al.*, 1991). It is interesting to compare these findings to an earlier behavioural study which demonstrated severe loss of ability to discriminate opposite DOM in cats reared in a stroboscopically illuminated environment (Pasternak and Leinen, 1986): such animals have been shown by single cell recording to lack directionally selective neurons in area 17 as well as higher visual areas, whereas in the case of the lateral suprasylvian cortex lesioned cats, such neurons in area 17 are unaffected (or at least not directly affected). The sensitivity of humans is lower to counterphase flicker than to drifting gratings (Levinson and Sekuler, 1975), the ratio being highest (always less than two) at low spatial and high temporal frequencies (Watson *et al.*, 1980). Pasternak (1986) showed that this relationship is not found in strobe reared cats, where sensitivity ratios are lower than in normal cats and unaffected by spatial or temporal frequency. Our results therefore also confirm that in our patients directionally selective mechanisms have not been compromised, providing further evidence that these patients do not resemble the deficit produced in cats by strobe rearing where directionally selective mechanisms in V1 are impaired.

One possible explanation for the preserved thresholds for the discrimination of DOM of sinusoidal gratings demonstrated in our cases and in cats having lateral suprasylvian cortex damage or macaques with MT/MST damage is that the lesions of extra-striate cortex are less complete than in patient LM. An alternative is that the cells in striate cortex selective for DOM can be accessed by other extra-striate visual areas. Forty percent of neurons in V3 of monkey are reported to be directionally selective (Fellman and Van Essen, 1987) and there is a substantial input to V4 which originates in the magnocellular pathway (Ferrera *et al.*, 1992), whereas inputs to V5-MT from the parvocellular pathway may be limited although not absent (Maunsell *et al.*, 1990).

While nearly 40 examples of complete achromatopsia have been published in the past 100 years (Zeki, 1990; Plant, 1991*b*) cases of profound subjective 'motion blindness' such as LM are very rare indeed (*see* Introduction). One possible explanation is that mechanisms subserving the perception of motion are less completely segregated than those subserving the perception of colour in extra-striate cortex. This is not to say that chromatic inputs to extra-striate areas, other than the cortical regions damaged in cerebral achromatopsia, do not exist but they do not subserve the perception of colour. A less interesting possibility is that infarction of lateral occipital cortex is more likely to cause a hemianopia than damage to the region of ventral occipito-temporal cortex which is damaged in cerebral achromatopsia. In support of this is the fact that the vascular accident sustained by LM is an unusual type (venous infarction) and our three cases had surgical damage. Of 35 cases of cerebral achromatopsia recently reviewed (Plant, 1991*b*), 25 were cases of arterial vascular occlusion.

It is worth noting that the deficit does not resemble the effect of damage to the magnocellular pathway at the level of the lateral geniculate nuclei in primates (Merigan *et al.*, 1991). In such animals contrast detection thresholds for sine-wave gratings were elevated and thresholds for direction and speed discrimination were elevated by the same

amount. That is to say, that any effect on motion perception of the lesion was a consequence of reduced visibility, not a deficit of motion perception itself. In the cases reported here the detection thresholds were not affected.

'Non-Fourier' or second-order motion

We have demonstrated that contrast thresholds for DOM discrimination of a CMod grating are elevated in the affected hemifields of Cases 1, 2 and 3. Why should this task differ from the DOM discrimination of a luminance modulated (LMod) grating? One possible explanation, which follows on from the above discussion, is that motion detectors at an early level, perhaps V1, respond only to changes in luminance and that a different mechanism or a second stage of motion processing is required to detect the DOM of a contrast modulation which does not contain contrast energy at the spatial frequency of the 'beat'. This concept has been developed recently by a number of workers employing a variety of such 'non-Fourier' motion stimuli (Lelkens and Koenderink, 1984; Derrington and Badcock, 1985; Derrington and Henning, 1987; Chubb and Sperling, 1988, 1989; Turano and Pantle, 1989; Pantle and Turano, 1992). Our finding that contrast thresholds for DOM discrimination of CMod gratings can be markedly impaired in cases where thresholds for DOM discrimination of LMod gratings are not affected (*see* Fig. 4) is compatible with the notion that regions of extra-striate visual cortex in the lateral occipital gyri are required for this task and for accurate speed discrimination, whereas DOM discrimination of LMod targets is processed at a lower level and this information may have access to extra-striate cortical areas unaffected by the damage in the cases reported here.

It should be noted that performance on the non-Fourier motion task employed in this study (DOM discrimination of a CMod grating) is poor in normal extra-foveal vision. This is likely to be true for a variety of non-Fourier motion tasks (*see*, for example, Pantle, 1992). We have employed a very low spatial frequency of contrast modulation because we found in preliminary experiments that the task was possible in normal peripheral vision at this low spatial frequency. Recent studies have confirmed that non-Fourier motion tasks are possible in human peripheral vision but that the mechanisms required to detect non-Fourier motion lose sensitivity faster as a function of eccentricity than mechanisms responsible for the detection of LMod stimuli (Solomon and Sperling, 1991).

Temporal frequency discrimination

The observation that Weber fractions for temporal frequency discrimination are also elevated across temporal frequency (Fig. 7, open symbols) is compatible with the notion that temporal frequency discrimination by humans is carried out by directional and velocity tuned mechanisms (Pasternak, 1987). This hypothesis suggests that, across a broad range of temporal frequency, humans cannot access a separate flicker mechanism which is separate from the motion system. However, there is a suggestion that LM (Hess *et al.*, 1989) may be able to carry out temporal frequency discrimination of counterphase gratings at high temporal rates where velocity discrimination is not possible. Therefore further observations are required to clarify this issue. This result may also be compared with findings in multiple sclerosis and optic neuritis (Plant and Hess, 1985; Plant, 1991*a*) where temporal frequency discrimination may be impaired only at high temporal rates. Here the pathology resides in the anterior visual pathways rather than cortex.

The characteristics of the residual motion perception

Two possible abnormalities of pursuit eye movements may be found following lesions of extra-striate cortex in primates and humans. A parietal lesion in humans may impair ipsilateral smooth pursuit (e.g. Morrow and Sharpe, 1990). An MST lesion in primates may give rise to a similar anomaly or lesions of V5-MT itself may produce a bidirectional pursuit deficit localized to the contralateral hemifield in primates (e.g. Dürsteler *et al.*, 1987) and there is a single reported human example which may represent the latter phenomenon (Thurston *et al.*, 1988). There is also evidence from studies of human congenital esotropia of anomalous motion processing of monocularly viewed stimuli moving in the nasal to temporal direction in either hemifield (Tychsen and Lisberger, 1986) which may represent a more 'primitive' motion system. Finally, there is evidence from studies of blindsight that cortical lesions may reveal the existence of visual mechanisms which show marked asymmetries between the crossed and uncrossed projections and which again could be more 'primitive' and may be mediated by subcortical mechanisms (e.g. Rafal *et al.*, 1990).

We have explored these possibilities in the experiments summarized in Fig. 6 and find no consistent evidence for any of these effects in our cases. Thus, from the point of view of previous studies of pursuit eye movements, although we have not recorded eye movements in our patients, we would suggest that the anomaly does not show a directional asymmetry and is localized to a hemifield and therefore most resembles the single case reported by Thurston *et al.* (1988). The most significant feature of the results shown in Fig. 7 is that the residual velocity discrimination in Case 1 varies as a function of both base velocity and contrast in the same way as in the ipsilateral hemifield. Thus, although the mechanisms concerned are degraded in some way, they may not represent the activity of fundamentally different mechanisms or pathways, as has been suggested in the case of the residual motion perception demonstrated in LM [where performance at direction and speed discrimination is relatively preserved at low temporal frequencies (Hess *et al.*, 1989); *see* Zihl *et al.* (1991) for further discussion of the physiological basis of the residual motion perception in LM]; in 'blindsight' or in esotropia. It is of particular theoretical importance that velocity discrimination does not improve at higher contrast levels: the deficit cannot be considered as equivalent to a threshold elevation in the contrast domain but represents a genuine impairment of mechanisms subserving the perception of velocity.

The results shown in Fig. 8 indicate that (as with LM; Hess *et al.*, 1989) temporal frequency discrimination is impaired in addition to velocity discrimination. Temporal frequency encoding does not necessarily require a mechanism that also encodes motion (i.e. one that encodes direction and speed), but these data are in agreement with results obtained in normal vision, which suggest that counterphase gratings are detected by directionally selective mechanisms across a wide range of spatial and temporal frequencies and that speed and temporal frequency may be processed by the same mechanisms [*see* Pasternak (1987) for a discussion of this issue]. We do not find evidence for a dissociation of velocity and temporal frequency processing.

ACKNOWLEDGEMENTS

This work was supported by the Medical Research Council of the United Kingdom and the Brain Research Trust.

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Received September 21, 1993. Revised August 16, 1993. Accepted September 14, 1993