

Movement in the normal visual hemifield induces a percept in the ‘blind’ hemifield of a human hemianope

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SUMMARY

We have investigated visual responses to moving stimuli presented to the normal hemifield of a hemianope, GY, who exhibits residual visual function in his right, ‘blind’ hemifield. Preliminary experiments established that his perception of moving stimuli localized in his ‘blind’ hemifield is retained when a similar stimulus is presented simultaneously in the normal hemifield. In response to a grating stimulus moving horizontally towards fixation in the non-foveal region of the normal, left hemifield, he perceives in addition to a normal motion percept in the left hemifield, a sensation of movement localized in the right hemifield. Qualitatively, this latter is indistinguishable from responses elicited by direct stimulation localized within his ‘blind’ hemifield by moving stimuli. We have investigated the characteristics of the mechanisms which induce the ‘blind’ field component of GY’s responses to stimulation of the normal hemifield. We show that GY’s sensitivity for detection of movement localized within his ‘blind’ hemifield is dependent on the direction of movement, the contrast and the velocity of a grating presented to the normal hemifield. No induced effects were recorded in response to colour or to non-moving, flickering stimuli. We examine the possible contribution of scattered light to our observations, and eliminate this factor by consideration of our experimental results. We discuss the neural mechanisms which may be involved in this response.

1. INTRODUCTION

There is an ordered representation of the visual field in the retinal projections to both the striate cortex and the superior colliculus of the macaque, and in both cases, each hemisphere receives its inputs from the contralateral hemifield. It has been reported that there is a strip of visual field, extending some 2° on either side of the vertical meridian, which is represented bilaterally in the macaque striate cortex (Stone *et al.* 1973; Bunt & Minckler 1977). The retinotopic representation in the prestriate cortical areas is also restricted to the contralateral hemifield (van Essen & Zeki 1978), although the large receptive fields of single neurones extend several degrees across the vertical meridian in areas V4 and V5 (Zeki 1978). The half-field representations of the two hemispheres are linked through the callosal fibres, which make connections restricted to the areas representing the vertical meridian (Myers 1962; Hubel & Wiesel 1968; van Essen & Zeki 1978). The callosal innervation in V1 is spatially localized, corresponding to the well defined representation of the vertical meridian, whereas in prestriate areas, V4 and V5, the innervation is diffuse, cor-

responding to the complex retinotopic mapping into these areas. The implications of these multiple transcallosal connections has been discussed by Zeki (1993). Neuronal receptive fields which receive extensive inputs from both visual hemifields are found in the temporal and parietal lobes (Bruce *et al.* 1986; Andersen 1987).

In humans, unilateral striate cortical damage results in visual field losses, which in extreme cases may involve the entire contralateral hemifield (hemianopia), although foveal sparing is frequently observed. Prestriate lesions of one hemisphere can result in loss of colour vision (achromatopsia) restricted to one hemifield (Verrey 1888; Damasio *et al.* 1980; Kölmel 1988) and other unilateral deficits of higher visual function have been reported (Ruddock 1991). Such observations are consistent with the retinotopic mapping described in the monkey. There is, however, less clear evidence regarding the retinotopic organization of human responses to movement. Positron emission tomography (PET) measurements (Zeki *et al.* 1991) and results of trans-cranial magnetic stimulation (Beckers & Hömberg 1992) suggest left hemispheric dominance, whilst impaired movement responses in patients with cortical damage indicate right hemispheric dominance (Vaina 1989). A recent study in this laboratory revealed non-retinotopic effects of motion

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on responses to colour which appeared to involve interhemispheric interactions (Morland *et al.* 1996*a*).

We have investigated further the characteristics of movement-sensitive visual mechanisms in a patient with extensive cortical damage involving the left striate and prestriate cortical areas. His visual fields for detection of non-transient light stimuli show a right homonymous hemianopia, with some 3.5° sparing around the fovea and a sharp step between the non-foveal sensitivities on either side of the vertical meridian (Barbur *et al.* 1980). GY is, however, sensitive to transient light stimulation of this 'blind' hemifield and is able to perform a number of visual discriminations on the basis of this residual visual function (Ruddock 1996). The cortical areas involved in these residual visual responses to light have yet to be identified, although a PET study has demonstrated activity in prestriate areas corresponding to macaque V3 and V5 (Barbur *et al.* 1993), and it has been suggested that the retino-collicular projections may also be involved (Barbur *et al.* 1980; Weiskrantz 1986, 1990). The initial studies on GY demonstrated that uniform illumination of the 'normal' hemifield exerts a small inhibitory influence on GY's sensitivity to transient lights presented within the 'blind' hemifield (Barbur *et al.* 1980). We decided, therefore, to examine the influence of moving stimuli presented to GY's normal, left hemifield on his detection of moving stimuli presented simultaneously to his right, 'blind' hemifield. We report that such stimulation does not inhibit GY's detection sensitivity in the 'blind' hemifield but yields evidence of bilateral activity in response to stimuli moving in his normal hemifield.

2. METHODS

(a) *Visual Stimuli*

All stimuli were generated with a three-channel Maxwellian view system (Barbur & Ruddock 1980) and unless otherwise stated, these were white light, of approximate colour temperature 3000 K. In those experiments requiring spectral stimuli, narrow bandwidth interference filters (Balzer B40) were placed in the light beams. The moving gratings were obtained by rotating in the different channels of the instrument radial, square-waveform gratings produced as photographic transparencies on high contrast Kodalith film. This method yielded high contrast (> 98%) gratings, which moved quasi-linearly across the visual field. The gratings rotated in the back focal plane of the imaging lens system, and the field size was controlled by a stop placed just before the rotating grating. The image of one such grating projected to the left hemifield, where it appeared within a rectangular area, the nearest edge of which was 6° from the fixation point and parallel to the vertical meridian (figure 1*a*). Another grating pattern was generated independently in a second channel of the Maxwellian view system and its image projected to the right hemifield (figure 1*a*). The speed of grating rotation was controlled by a variable speed motor and the direction of grating motion was adjusted by changing the point in space around which the grating rotated. A set of photographic transparencies, matched for image contrast, provided gratings of different periodicities. A fixation point, F, was produced as a dark spot on an otherwise clear photographic transparency, and placed in the

third channel. The field size produced by this beam was controlled by placing appropriate stops in the back focal plane of the imaging lens system and the resulting uniform illumination either flooded the whole of the visual field except for the area covered by the grating in the left hemifield (figure 1*a*), or it occupied a central vertical strip, which extended $\pm 5^\circ$ from the fixation point (figure 3*b*). All light levels were controlled by neutral density filters and the duration of stimulus presentation by electromagnetic shutters with rapid (< 10 ms) opening and closing actions. Stimulus parameters including dimensions, duration of presentation, the velocity and direction of the grating movements and all luminance levels were calibrated *in situ*, through the exit pupil of the system. Luminance levels were calibrated with a Macam radiometer/photometer. The system generated extremely well defined stimuli, and no stray light associated with presentation of the grating to the left hemifield was detectable in the right hemifield.

(b) *Procedures*

The observer used a bite bar to maintain the eye pupil centrally with respect to the 3 mm instrumental exit pupil, and he controlled the time at which the stimulus was presented by pressing a response button. Stimulus duration was 1 s, during which time the observer fixated on the central point F (figure 1*a*). We did not monitor eye movements continuously, but GY maintains good fixation to within $\pm 1^\circ$ over periods of several seconds (Morland *et al.* 1996*b*). The observer responded verbally after each presentation, and in a given experiment, stimuli of different luminances were each presented a fixed number of times (usually five) in random sequence. The observer reported whether presentation of a stimulus generated a percept localized in the right hemifield and whether that percept was one of movement or of non-movement. This latter distinction was introduced by the patient GY during the preliminary observations (see results). The direction of movement of the grating stimuli was identified unambiguously by normal observers and by GY when they were presented in his normal hemifield. All measurements were preceded by 15 min dark adaptation.

(c) *Observers*

The principal subject of this study was GY, a 38-year-old male who has a right homonymous hemianopic field loss associated with neuronal damage involving the left geniculostriate projection fibres, and the striate and prestriate areas of the left hemisphere (Barbur *et al.* 1993; Brent *et al.* 1994). His field plot for stationary stimuli reveals sparing in the 'blind' hemifield to 3.5° around fixation (Barbur *et al.* 1980) and the sharp division between his seeing and 'blind' hemifields is indicative of restricted bilateral representation at the vertical meridian. GY has residual vision which gives a percept in response to transient light stimulation of his 'blind' hemifield, enabling him to localize the stimulus and to perform a variety of discriminations. His residual responses to transient stimuli have been described in several previous papers (Barbur *et al.* 1980, 1994; Blythe *et al.* 1986, 1987; Morland *et al.* 1996*b, c*) and it is his ability to detect stimulus movement which is relevant to the present study. GY, like some other hemianopic patients (Stoerig & Cowey 1992), can perform limited chromatic discriminations using his residual vision (Brent *et al.* 1994). In addition to his residual vision, GY can use a 'blind sight' response mode to discriminate between light stimuli (Weiskrantz *et al.* 1995), but our present investigation was restricted to GY's residual responses. Observations were

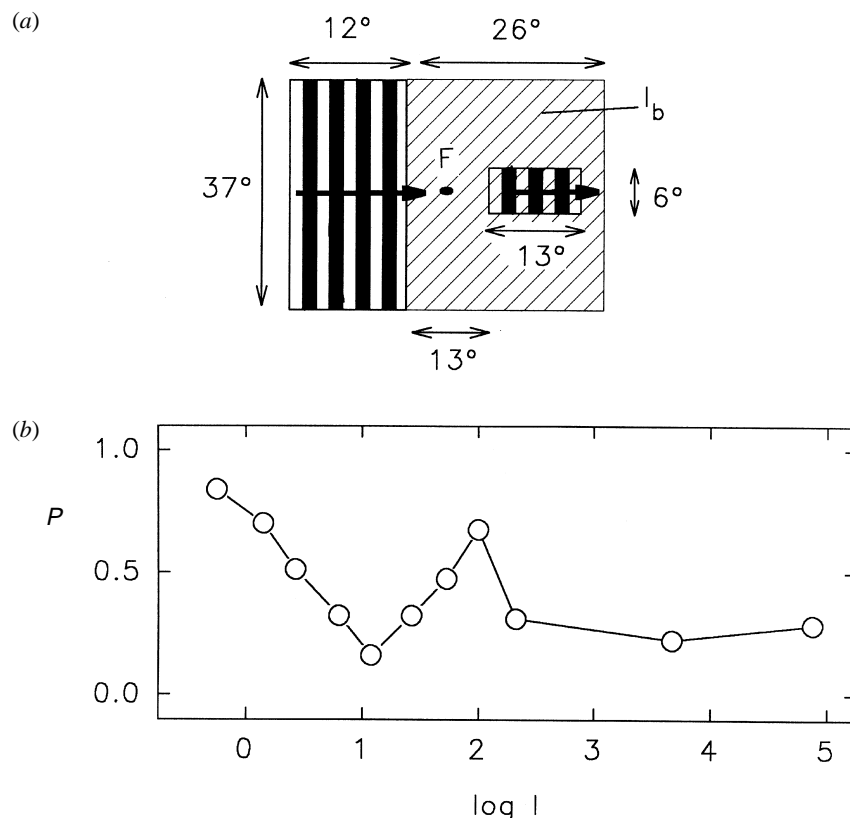


Figure 1 (*a*). The field configuration used to determine whether GY can detect simultaneously, movement in both hemifields. The square-waveform gratings (periodicity $0.4 \text{ cycles deg}^{-1}$) moved in the direction indicated (left to right) at 24 deg s^{-1} , their mean luminance was 2 log trolands and duration of presentation was 1 s . The hatched area was uniformly illuminated at 2 log trolands (I_b), and the fixation point, F, was midway between the two gratings. All stimuli were white light (colour temperature 3000 K). (*b*) The probability P of GY's detecting a percept localized in the blind hemifield and in the direction right to left, plotted against the luminance, I , of the smaller grating located to the right of fixation (*a*). Each I value was presented five times, in a random sequence.

made by a group of nine normal naive observers, four male and five female, with ages between 22 years and 35 years and by a second hemianope, EB, a female aged 38 years who lacked residual vision in her blind right hemifield.

3. RESULTS

(*a*) Preliminary observations

We firstly established that GY was able to detect two moving stimuli presented simultaneously, one to each hemifield, for the stimulus configuration shown in figure 1 *a*. In response to such stimuli, GY reported two distinct motion percepts, one localized in the normal hemifield and the other in the 'blind' hemifield. The two percepts differed markedly in quality, that in the 'blind' hemifield being described as a dark shadow, characteristic of GY's residual vision, whilst that in the normal hemifield was normal. With the grating bars orientated horizontally and moving vertically, we varied the luminance of the grating in the 'blind' hemifield to find threshold for its detection, the mean grating luminance in the normal field being maintained at 2.0 log trolands . With the left grating moving at 32 deg s^{-1} , the luminance of the right, moving grating required for threshold detection was $3.1 \pm 0.1 \text{ log trolands}$; with the left grating stationary it was $3.1 \pm 0.1 \text{ log trolands}$ and with the left grating removed it was $3.0 \pm 0.1 \text{ log trolands}$, thus the presence of the

moving grating in the normal hemifield had no effect on detection of the moving grating presented to the 'blind' hemifield. With the grating bars in both hemifields orientated vertically and moving horizontally left to right (figure 1 *a*), however, GY reported movement localized in the 'blind' hemifield, whatever the luminance of the right hand grating, but for low luminances of this latter he usually reported the movement as right to left. He was unable to differentiate between the locations of the left-right and right-left motion percepts in the right hemifield, describing them as occurring in approximately the same position. We did not in these experiments attempt to determine accurately the relative locations of the two percepts. The probability with which GY identified the movement in the blind hemifield as directed right to left is plotted in figure 1 *b* as a function of the luminance of the right-field grating, and the incidence of right-left responses increases as the luminance is reduced. This unexpected response is, therefore, associated with the stimulus presented to the left hemifield rather than with that presented to the 'blind' hemifield itself. GY experienced difficulty, however, in identifying the direction of movement with these grating stimuli, and in most of the remaining experiments we measured threshold for detection of a motion percept, localized in the right hemifield, associated with presentation of a moving grating in the

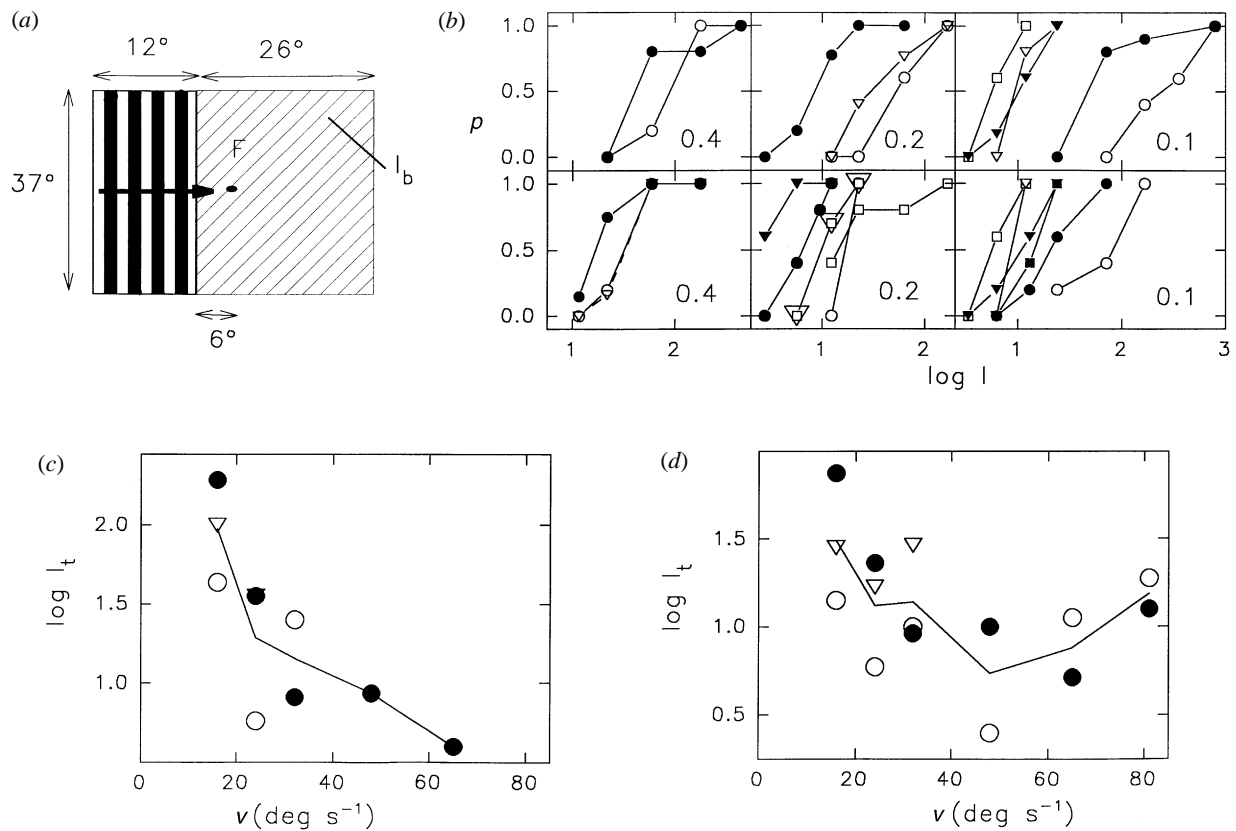


Figure 2 (*a*). The stimulus configuration used to determine the dependence of GY's 'blind' field response sensitivity on the velocity and spatial periodicity of the grating presented to the normal hemifield. The observer fixated at F and the luminance of the hatched area, I_b , was 2 log trolands. All stimuli were white light, and presented for 1 s. (*b*) The probability of GY's detecting a percept of movement (upper row) or any percept (lower row) in the right hemifield, plotted against the mean luminance, I , of the moving grating shown in (*a*). The grating periodicity is noted, in cycles deg^{-1} , at the lower right of each panel. Each symbol denotes a different drift velocity, left to right: \circ 16 deg s^{-1} ; \bullet 24 deg s^{-1} ; ∇ 32 deg s^{-1} ; \blacktriangledown 48 deg s^{-1} ; \square 65 deg s^{-1} ; \blacksquare 80 deg s^{-1} . Each I value was presented five times, in random sequence. (*c*) The threshold mean luminance, I_t , at which GY achieved 0.5 probability in detecting movement localized in his 'blind' hemifield, plotted against the grating velocity, v . Values derived from the data given in the upper row of (*b*). Each symbol denotes a different grating periodicity: \bullet 0.1 cycles deg^{-1} ; \circ 0.2 cycles deg^{-1} ; ∇ 0.4 cycles deg^{-1} . As in all such plots, the error in I_t associated with each data point arising from the statistical variance in the probability values, is comparable to the height of the symbols. (*d*) As (*c*) but I_t corresponds to the mean grating luminance at which GY achieved 0.5 probability of detecting any percept in the 'blind' hemifield.

normal, left hemifield, without reference to direction of movement. GY reported that in such experiments, the stimulus sometimes elicited in the 'blind' hemifield a sensation of flicker or of a flash, without associated movement. We therefore permitted three responses for each stimulus presentation, namely movement, non-movement (flicker or flash) or no percept. The remaining data are presented with reference to the parameters of the stimulus presented to the normal, left hemifield.

(b) Grating velocity

We measured responses with the stimulus configuration of figure 2*a*, for grating bars orientated vertically and moving left to right, towards fixation. The velocity of the bars was varied between experiments and for each velocity, the grating was set at a series of luminance levels, in random sequence, each presented for 1 s. GY was asked to identify any percept localized in the 'blind' hemifield as moving or stationary, or to state if no percept was detected.

Measurements were made for three different spatial periodicities of the moving grating and the probability of GY's detecting movement and that of detecting any percept are plotted against stimulus luminance in figure 2*b*. Threshold response functions derived from these results are plotted as a function of stimulus velocity in figure 2*c, d*. Neither the nine normal subjects nor the second hemianope detected any activity localized in the hemifield contralateral to the stimulus, even when the uniform masking field shown in figure 2*a* was removed.

(c) Grating contrast

The mean luminance of the left hemifield grating required for GY to detect a percept in the right, 'blind' hemifield was measured with the stimulus configuration of figure 3*a*. Measurements were made with the moving grating (spatial frequency 0.4 cycles deg^{-1} ; velocity 24 deg s^{-1}) superimposed on a uniform background, the luminance of which, I_b , varied between experiments. For each I_b value, the grating was

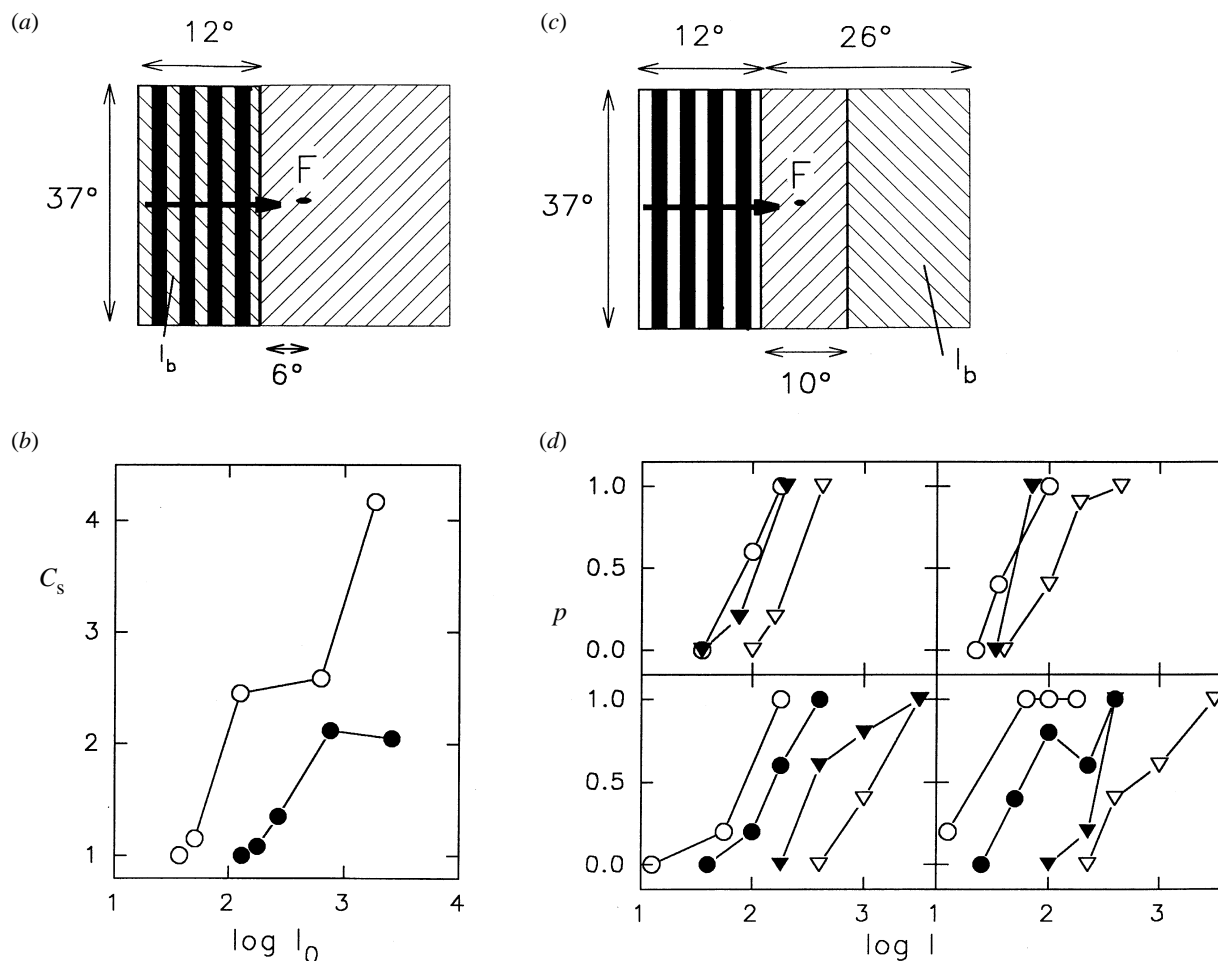


Figure 3 (*a*). The stimulus configuration used to find the dependence of GY's 'blind' field response on the contrast of the grating (periodicity $0.4 \text{ cycle deg}^{-1}$; velocity 24 deg s^{-1}). The grating was superimposed on a uniform background of luminance I_b , which was fixed at a different value for each experiment. In each experiment, P was measured as a function of the mean grating luminance I , to yield data similar to those shown in figure 2 (*b*). The uniform field to the right of the grating was of fixed luminance $2 \log$ trolands. All stimuli were white light, and the moving gratings were presented for 1 s. (*b*) The contrast sensitivity, C_s , at which GY achieved 0.5 probability of detecting a movement percept (●) or any percept (○), plotted against the mean luminance of the grating plus background stimulus. C_s is defined as C_t^{-1} , where C_t is the contrast corresponding to $P = 0.5$. Contrast C is defined by the Michelson expression. (*c*) The stimulus configurations used to obtain the data of (*d*) (upper row). The grating (periodicity $0.4 \text{ cycle deg}^{-1}$; velocity 24 deg s^{-1}) was set at 100% contrast. The central strip, width 10° , was set at $2 \log$ trolands, and the right field was illuminated at luminance I_b . At each I_b value, GY's responses were measured for different mean luminances, I , of the grating. (*d*) The probability p , of GY's detecting movement (left-hand data sets) or any percept (right-hand data sets) plotted against the mean grating luminance I (trolands). The upper row refers to the stimulus configuration of (*c*), and the lower to the stimulus configuration of (*a*). Each data set corresponds to a different I_b value: ● $-0.6 \log$ trolands; ▼ $1.8 \log$ trolands; ▽ $3.0 \log$ trolands; ○ zero background luminance.

presented for 1 s at a series of mean luminance levels I , selected in random sequence. After each presentation, GY was asked to identify any percept induced in the right hemifield as moving or stationary, or to state if no percept occurred. The results for grating movement directed from left to right in the normal hemifield (i.e. towards fixation) are plotted as contrast sensitivity against mean grating luminance (figure 3*b*). A similar experiment was performed with the field configuration of figure 3*c*, in which the 'blind' hemifield is illuminated with a uniform field at luminance I_b , except for a strip around the vertical meridian, which was at fixed luminance ($2 \log$ trolands). The results of this experiment, expressed as probability for detection of a percept in the 'blind' hemifield plotted against I ,

the mean luminance of the grating presented to the normal hemifield (figure 3*d*), show that uniform illumination in the 'blind' hemifield has less effect on GY's responses than equivalent illumination of the normal hemifield. This result enables us to discount scattered light as a factor in the response (see Discussion).

(*d*) Grating orientation

The moving grating (spatial frequency $0.4 \text{ cycles deg}^{-1}$; velocity 24 deg s^{-1}) was presented to the left hemifield in the configuration shown in figure 2*a*, but the orientation of the grating bars was varied between experiments, and in each case movement was normal

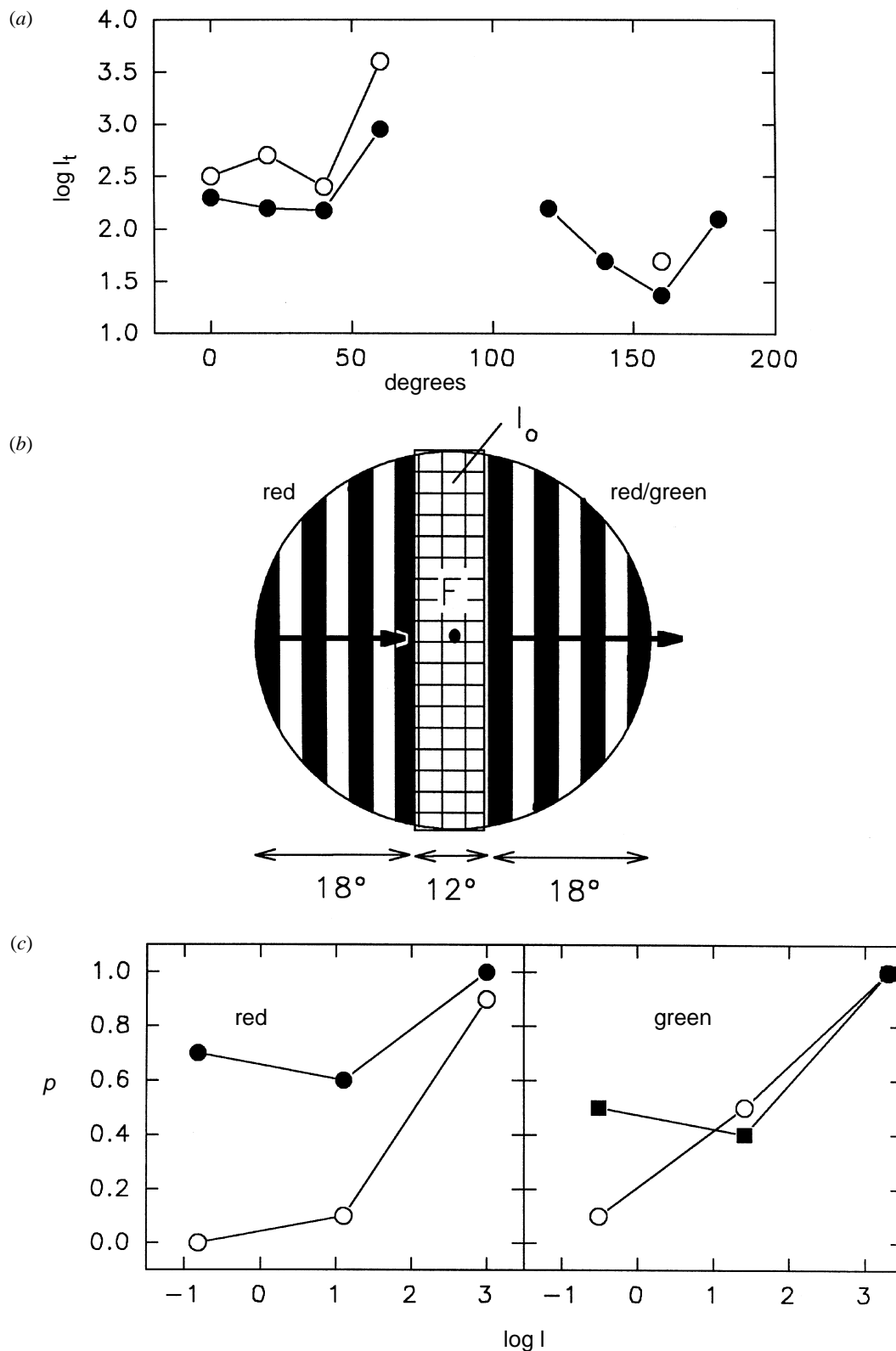


Figure 4(a). The mean luminance, I_t , of the grating stimulus (periodicity $0.4 \text{ cycle deg}^{-1}$; velocity 24 deg s^{-1}) at which GY achieved 0.5 probability of detecting motion (○) or any percept (●) in his 'blind' hemifield. Stimulus configuration as in figure 2(a), but the angle, θ , at which the grating moved, with its bars orthogonal to the direction of movement, was varied. $\theta = 0^\circ$ corresponds to horizontal movement towards the fovea and $\theta = 180^\circ$ to horizontal movement away from the fovea. Luminance detection thresholds for θ equal to 80° and 100° were greater than the maximum available luminance of 4 log trolands. (b) The stimulus in the left hemifield was red (655 nm) and that in the right 'blind' hemifield was either red (655 nm) or green (542 nm). Both gratings moved left to right at 48 deg s^{-1} and were of periodicity $0.4 \text{ cycles deg}^{-1}$. The central 12° strip was white light, of luminance 2 log trolands, and the fixation point, F, was centrally located between the gratings. The colour and mean luminance of the right-hand grating

to the bar orientation. For each orientation, the grating was presented at a series of mean luminances selected in random sequence, and GY was asked to state whether a 1 s presentation of the moving grating induced a percept localized to the right hemifield, and if so, whether or not he detected movement. The results (figure 4*a*) show that induced movement was much more readily detected for grating movement towards fixation than for movement in the opposite direction. In the former case, the motion percept in the 'blind' hemifield was usually described as being towards fixation. In contrast, sensitivity for detection of any percept, moving or not, does not exhibit such asymmetry.

(e) Colour and flicker

We examined the percept induced in GY's 'blind' hemifield by a moving, coloured grating with the stimulus configuration shown in figure 4*b*. This consisted of a red grating of fixed mean luminance (3 log trolands) presented for 1 s to the normal hemifield together with a red or green grating, each set at one of three mean luminances, presented to the 'blind' hemifield (figure 4*b*). The six different 'blind' field stimuli were each presented ten times in random sequence, and following each presentation, GY was asked to identify both the colour ('red' or 'green') and direction of movement ('left-right' or 'right-left') of the percept localized in the blind hemifield, which was detected on every presentation. The probabilities of his identifying the percept as being the colour of the 'blind' field grating and as moving 'left-right' are plotted against the luminance of the 'blind' field grating (figure 4*c*). At the highest luminance he detects the colour as that of the 'blind' field stimulus, but as luminance is reduced, his colour naming becomes essentially random ($p = 0.5$). His identification of movement direction, however, reverses from 'left-right' at the highest luminance to 'right-left' at the lowest luminance, as was found in the preliminary observations (figure 1*b*). With the 'blind' field stimulus at low luminances, GY detects the percept induced in the 'blind' field by the grating in the normal field, and the results of figure 4*c* show that whereas the direction of perceived motion is reversed relative to that of the inducing stimulus, there is no consistent colour associated with the percept. GY detected no percept in the 'blind' field associated with presentation in the normal hemifield of uniform flicker at 2 Hz to 10 Hz.

4. DISCUSSION

The preliminary experiments establish that GY can detect and localize two moving stimuli presented simultaneously, one in each hemifield. For horizontal

movement directed towards the fovea, stimulus motion in the normal left hemifield generates a percept of motion, again directed towards the fovea in the 'blind' hemifield (figure 1*b*; figure 4*c*). Previous observations (Barbur *et al.* 1980) indicated that uniform illumination of the normal hemifield exerts a weak inhibitory effect on GY's detection of transients presented to the 'blind' hemifield, but our new observations show that movement in the normal hemifield can generate a motion percept localized in the 'blind' hemifield which is qualitatively indistinguishable from that associated with direct stimulation of the 'blind' hemifield. This percept is apparently weak, as GY cannot distinguish it from that generated by direct stimulation of the 'blind' field unless the latter is at low luminance (figure 1*b*, figure 4*c*). The effect is specifically associated with movement as GY reported no 'blind' field percept in response to flicker or colour (figure 4*c*).

The effectiveness of the left-field stimulus in inducing a movement percept in the contralateral field is directionally selective, being in most cases much greater for horizontal movement towards the fovea than for vertical movement, or for horizontal movement away from the fovea (figure 4*a*). In contrast, sensitivity for detection without regard to movement is similar for both horizontal directions of stimulus motion (figure 4*a*). Previous measurements with GY have revealed higher sensitivity for detection of horizontal movement than for near vertical movement (Ruddock 1991, fig. 11.6), but similar sensitivities were observed for both directions of horizontal movement (Barbur *et al.* 1980; Blythe *et al.* 1986).

Our results illustrate other properties of the 'blind' field response induced by movement in the normal hemifield which are similar to those produced by direct stimulation of the 'blind' field. Response sensitivity increases as velocity increases, being too low to measure at values below 16 deg s⁻¹ (figure 2*c*), and the velocity dependence is very similar to that found by Barbur *et al.* (1980) in measurements with a moving spot presented directly to GY's 'blind' hemifield. We did not in these experiments determine the upper velocity limit of the response. Like GY's responses to direct stimulation of the 'blind' hemifield, the induced response is observed only with high contrast stimuli and is uncharacteristic of the M-type retinal projection signals, which saturate at low contrast (Shapley *et al.* 1981).

In these experiments, illumination of GY's 'blind' hemifield at 2 log trolands minimized the effects of any light scattered into the 'blind' hemifield, either within the Maxwellian view optical system or intra-ocularly. GY has normal levels of intra-ocular scatter (Barbur *et al.* 1994), thus the fact that normal subjects reported no induced response provides strong evidence that GY is

were changed randomly from presentation to presentation (duration 1 s) and each condition was presented ten times. (c) The probability, P, of GY's detecting the movement percept in the right, 'blind' hemifield (○ circles) as being from left to right plotted against the mean luminance, I (log trolands), of the right hand grating. Such a movement percept was reported for all stimulus presentations. Those data which refer to presentation of a red grating in the right hemifield are plotted separately from those obtained when it was green, as marked. The probabilities with which GY named correctly the colour of the right-hand grating are given as full circles or squares.

not detecting intra-ocular scatter, especially as all studies on him have found sub-normal sensitivity in his detection of stimuli presented to the 'blind' hemifield. This conclusion is confirmed by the observation that uniform illumination of the 'blind' hemifield has less effect on GY's detection of a 'blind' field percept than does equivalent illumination of the normal hemifield (figure 3*d*). We show formally in the Appendix that were GY's induced 'blind' field response due to scattered light, this last result would be impossible.

Anatomical and physiological observations demonstrate that retinotopic mapping into the striate and prestriate visual cortical areas of one hemisphere represents essentially the contralateral hemifield. Our stimulus configuration (e.g. figure 1*a*) eliminates any possible contribution from the bilaterally represented vertical strip described for the macaque (Stone *et al.* 1973; Bunt & Minckler 1977) and further, we were able to induce the percept with a moving grating located in the normal hemifield as in figure 2*a*, but with its nearest edge 20° from fixation. Callosal fibres provide for interhemispheric signal transmission at the vertical meridian, and we plan further measurements in order to check whether this pathway is implicated in GY's induced 'blind' field responses. Bilaterally driven visual neurones in the temporal and parietal lobes could contribute to GY's responses. GY's detection of the induced percept to movement is predominantly generated by movement in the normal hemifield directed towards the fovea. Neurones which respond selectively to radial movement, the majority to inwardly directed movement, have been observed in the monkey parietal lobe (Steinmetz *et al.* 1987).

Moving stimuli presented to GY's 'blind' hemifield failed to induce a percept in his normal hemifield, and no corresponding phenomenon was reported by the normal controls. Thus, like certain other features of GY's residual vision, such as extensive spatial summation in threshold detection (Barbur *et al.* 1980), the responses described in this paper indicate that he has access to light-activated mechanisms which do not contribute to normal, conscious vision. Such activity may be suppressed in the presence of the normal geniculostriate contribution, or may reflect functional reorganization consequent on his left hemispheric lesions.

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REFERENCES

- Andersen, R. A. 1987 Inferior parietal lobule function in spatial perception and visuomotor integration. In *Handbook of physiology. The nervous system. Higher functions of the brain*. Section I, vol. v, part 2, ch. 12. pp. 483–518. Bethesda: American Physiology Society.
- Barbur, J. L. & Ruddock, K. H. 1980 Spatial characteristics of movement detection mechanisms in human vision. I. Achromatic vision. *Biol. Cybern.* **37**, 77–92.
- Barbur, J. L., Ruddock, K. H. & Waterfield, V. A. 1980 Human visual responses in the absence of the geniculocalcarine projection. *Brain* **103**, 905–928.
- Barbur, J. L., Watson, J. D. G., Frackowiak, R. S. J. & Zeki, S. 1993 Conscious visual perception without VI. *Brain* **116**, 1293–1302.
- Barbur, J. L., Harlow, A. J. & Weiskrantz, L. 1994 Spatial and temporal response properties of residual vision in a case of hemianopia. *Phil. Trans. R. Soc. Lond. B* **343**, 157–166.
- Beckers, G. & Hömberg, V. 1992 Cerebral visual motion blindness: transitory akinetopsia induced by transcranial magnetic stimulation of human area V5. *Proc. R. Soc. Lond. B* **249**, 173–178.
- Blythe, I. M., Bromley, J. M., Kennard, C. & Ruddock, K. H. 1986 Visual discrimination of target displacement remains after damage to the striate cortex in humans. *Nature, Lond.* **320**, 619–621.
- Blythe, I. M., Kennard, C. & Ruddock, K. H. 1987 Residual vision in patients with retrogeniculate lesions of the visual pathways. *Brain* **110**, 887–905.
- Brent, P. J., Kennard, C. & Ruddock, K. H. 1994 Residual colour vision in a human hemianope: spectral responses and colour discrimination. *Proc. R. Soc. Lond. B* **256**, 219–225.
- Bruce, C. J., Desimone, R. & Gross, C. G. 1986 Both striate cortex and superior colliculus contribute to visual properties of neurons in superior temporal polysensory area of macaque monkey. *J. Neurophysiol.* **55**, 1057–1075.
- Bunt, A. H. & Minckler, D. S. 1977 Foveal sparing. *Arch. Ophthalmol.* **95**, 1445–1447.
- Damasio, A., Yamadu, T., Damasio, H., Corbett, J. & McKee, J. 1980 Cerebral achromatopsia: behavioural, anatomic and physiological aspects. *Neurology* **30**, 1064–1071.
- Hubel, D. H. & Wiesel, T. N. 1968 Receptive fields and functional architecture of monkey striate cortex. *J. Physiol. Lond.* **195**, 215–243.
- Kölmel, H. W. 1988 Pure homonymous hemiachromatopsia: findings with neuro-ophthalmologic examination and imaging procedures. *Eur. Arch. Psychiat. Neurol. Sci.* **237**, 237–243.
- Morland, A. B., Ogilvie, J. A., Ruddock, K. H. & Wright, J. R. 1996*a* A new abnormality of human vision provides evidence of interactions between cortical mechanisms sensitive to movement and those sensitive to colour. *Proc. R. Soc. Lond. B* **263**, 1087–1094.
- Morland, A. B., Ogilvie, J. A., Ruddock, K. H. & Wright, J. R. 1996*b* Orientation discrimination is impaired in the absence of the striate cortical contribution to human vision. *Proc. R. Soc. Lond. B* **263**, 633–640.
- Morland, A. B., Ogilvie, J. A. & Ruddock, K. H. 1996*c* Second order motion is detected by a hemianopic patient in the absence of geniculostriate input. *J. Physiol. Lond.* **497**, 62.
- Myers, R. E. 1962 Commissural connections between occipital lobes of the monkey. *J. Comp. Neurol.* **118**, 1–16.
- Ruddock, K. H. 1991 Spatial vision after cortical lesions. In *Vision and visual dysfunction*, vol. 10. *Spatial vision* (ed. D. Regan), 261–289. Basingstoke: Macmillan.
- Ruddock, K. H. 1996 Residual visual function in the absence of the human striate cortex. In *Basic and clinical perspectives in vision research* (ed. M. B. A. Djamgoz & J. Robbins), pp. 211–224. London: Plenum.
- Shapley, R., Kaplan, E. & Soodak, R. 1981 Spatial summation and contrast sensitivity of X and Y cells in the lateral geniculate nucleus of the macaque. *Nature, Lond.* **292**, 543–545.
- Steinmetz, M. A., Motter, B. C., Duffy, C. J. & Mountcastle, V. B. 1987 Functional properties of parietal visual

- neurons: radial organization of directionalities within the visual field. *J. Neurosci.* **7**, 177–191.
- Stoerig, P. & Cowey, A. 1992 Wavelength discrimination in blindsight. *Brain* **115**, 425–444.
- Stone, J., Leicester, J. & Sherman, S. M. 1973 The naso-temporal division of the monkey's retina. *J. Comp. Neurol.* **150**, 333–348.
- Vaina, L. M. 1989 Selective impairment of visual-motion interpretation following lesions of the right occipitoparietal area in humans. *Biol. Cybern.* **61**, 347–349.
- Verrey, D. 1888 Hémichromatopsie droite absolue. Conservation partielle de la perception lumineuse et des formes. Ancien kyste hémorragique de la partie inférieure du lobe occipital gauche. *Arch. Ophthalmol. Paris* **8**, 289–300.
- Van Essen, D. C. & Zeki, S. M. 1978 The topographic organization of rhesus monkey prestriate cortex. *J. Physiol. Lond.* **277**, 193–226.
- Weiskrantz, L. 1986 *Blindsight: a case study and implications*. Oxford University Press.
- Weiskrantz, L. 1990 The Ferrier Lecture 1989. Outlooks for blindsight; explicit methodologies for implicit processes: *Proc. R. Soc. Lond. B* **239**, 247–278.
- Weiskrantz, L., Barbur, J. L. & Sahaie, A. 1995 Parameters affecting conscious versus unconscious visual discrimination with damage to the visual cortex (VI). *Proc. Natn. Acad. Sci. USA* **92**, 6122–6126.
- Zeki, S. M. 1978 Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *J. Physiol. Lond.* **277**, 273–290.
- Zeki, S. 1993 *A vision of the brain*. Oxford: Blackwell
- Zeki, S., Watson, J. D. G., Lueck, C. J., Friston, K. J., Kennard, C. & Frackowiak, R. S. J. 1991 A direct demonstration of functional specialization in human visual cortex. *J. Neurosci.* **11**, 641–649.

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APPENDIX

For a 1-D grating stimulus of modulation depth M and mean luminance I_0 , the contrast is given by $M/2I_0$. Let the effects of light scatter into the 'blind' hemifield of such a grating presented to the normal hemifield give rise to a grating structure with contrast given by

$$\frac{fM}{2f'I_0},$$

where $f(\ll 1)$ represents the reduced grating contrast and $f'(\ll 1)$ the reduced overall luminance in the scattered image. Consider addition of a uniform field, luminance I_b , to the normal hemifield. Then the scattering process will produce a grating contrast

$$\frac{fM}{2f'(I_0 + I_b)}$$

in the 'blind' hemifield. If, however, the uniform field is added to the 'blind' field, the modified contrast becomes

$$\frac{fM}{2(f'I_0 + I_b)}.$$

The experimental data (figure 3*d*) show that the latter is the more effective moving stimulus, and this requires that its contrast, which describes the moving component, is the greater, i.e.

$$\begin{aligned} \frac{fM}{2(f'I_0 + I_b)} &> \frac{fM}{2f'(I_0 + I_b)}, \\ \therefore 2f'I_0 + 2f'I_b &> 2f'I_0 + 2I_b, \\ \text{i.e. } f' &> 1. \end{aligned}$$

Thus the experimental results imply a scattering coefficient of greater than unity. The minimum distance from the stimulus in the normal hemifield to GY's blind hemifield is 5° (figure 3*a*) and in their measurements on GY, Barbur *et al.* (1994) were unable to detect significant light scatter at angles greater than 5° from a 2 log troland glare source.