Brain (1999), **122,** 1183–1198

Visual perception of motion, luminance and colour in a human hemianope

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Summary

Human patients rendered cortically blind by lesions to V1 can nevertheless discriminate between visual stimuli presented to their blind fields. Experimental evidence suggests that two response modes are involved. Patients are either unaware or aware of the visual stimuli, which they are able to discriminate. However, under both conditions patients insist that they do not see. We investigate the fundamental difference between percepts derived for the normal and affected hemifield in a human hemianope with visual stimuli of which he was aware. The psychophysical experiments we employed required the patient, GY, to make comparisons between stimuli presented in his affected and normal hemifields. The subject discriminated between, and was allowed to match, the stimuli. Our study reveals that the stimulus parameters of colour and motion can be discriminated and matched between the normal and blind hemifields, whereas brightness cannot. We provide evidence for associations between the percepts of colour and motion, but a dissociation between the percepts of brightness, derived from the normal and hemianopic fields. Our results are consistent with the proposal that the perception of different stimulus attributes is expressed in activity of functionally segregated visual areas of the brain. We also believe our results explain the patient's insistence that he does not see stimuli, but can discriminate between them with awareness.

Keywords: blindsight; scotoma; vision; V1; cortical blindness

Introduction

Unilateral lesions of the primary visual cortex (V1) result in scotomata of the visual hemifield contralateral to the lesion. Where the lesion is complete, patients are described as homonymous hemianopes. The occipital pole can escape lesion, perhaps because it is within the watershed zone between the posterior and middle cerebral arteries, and in such cases macular sparing of the visual field is observed. When tested within the area of scotoma, patients are shown to be clinically blind to the static targets presented during perimetry.

However, psychophysical tests have revealed considerable residual function in the blind hemifields of some hemianopes. Initial investigations demonstrated that patients were able to loçalize briefly presented flashes in the hemianopic field (Poppel *et al.*, 1973; Weiskrantz *et al.*, 1974). Subsequent studies have focused on the characterization of the residual responses. The main approach has been to require the patient to discriminate between two visual stimuli. Such forced choice studies have revealed that all patients with responses to light have elevated luminance thresholds for transiently presented stimuli (Barbur *et al.*, 1980; Blythe *et al.*, 1987; Stoerig and Cowey, 1991, 1992; Weiskrantz, 1998). Discriminations between moving stimuli have been shown to be the least affected responses, with discrimination thresholds at or very near those of normal observers (Barbur *et al.*, 1980; Blythe *et al.*, 1986; Perenin, 1991). For discriminations between coloured stimuli, however, responses of hemianopes are impoverished compared with those of normal controls (Blythe *et al.*, 1987; Stoerig and Cowey, 1992; Brent *et al.*, 1994). Spatial discrimination between sine wave gratings has been reported for some subjects (Weiskrantz *et al.*, 1974), whereas other investigations have failed to reveal such a function psychophysically (Barbur *et al.*, 1980). Orientation discrimination is worse than normal (Weiskrantz, 1986), and, in one patient, was found on tests with single line boundaries but not gratings (Morland *et al.*, 1996).

In addition to the studies on human patients, there is also literature on behavioural responses of monkeys with V1 lesions, which has recently been reviewed by Stoerig and Cowey (Stoerig and Cowey, 1997). Destriate monkeys can localize targets presented within their scotomata (Keating,

1975; Mohler and Wurtz, 1977) and also make discriminations on the basis of luminance and brightness (Schilder *et al.*, 1972). Orientation (Keating, 1975) and colour (Schilder *et al.*, 1972; Keating, 1979) discriminations have also been measured, and both are degraded compared with normal thresholds. Thus, a very similar pattern of results from human and monkey studies has been revealed (Stoerig and Cowey, 1997).

In the absence of V1, other visual areas must mediate the visual abilities of both hemianopic humans and monkeys. The visual projections that are not destined for V1 arise from two principal sources, namely the dorsal lateral geniculate nucleus and the pulvinar via the superior colliculus. Using anatomical staining techniques, direct projections from the dorsal lateral geniculate nucleus to prestriate areas have been shown to target V2, V3 and V4 (Benevento and Yoshida, 1981; Yukie and Iwai, 1981; Stoerig and Cowey, 1989). The projections via the superior colliculus exhibit cone input, and spectral opponency is observed in the pulvinar (Felsten *et al.*, 1983), so some P-type projection to subcortical structures is likely. Electrophysiological measurements have demonstrated continued activity of neurons in V5/MT (Girard *et al.*, 1992) and V3 (Girard *et al.*, 1991) following lesion or reversible cooling of V1. However, activity in V5 was not found on subsequent lesion of the superior colliculus (Rodman *et al.*, 1990). Functional imaging studies have revealed significant activity in prestriate areas of human hemianopes (Baseler *et al.*, 1999), with particularly robust responses in V3 and V5 (Barbur *et al.*, 1993; Zeki and ffytche, 1998). Furthermore, recent studies have documented activity in the superior colliculus during stimulation of the hemianopic field (Sahraie *et al.*, 1997; Barbur *et al.*, 1998).

The features of the residual visual capacities in human hemianopes and monkeys with lesions to V1 appear to be consistent with the properties of the visual pathways that remain in the absence of V1. Thus, patients are little affected when their discriminations are made on the basis of transience or motion, which are stimulus attributes encoded by the M-type system (Merigan *et al.*, 1991) and probably areas in the dorsal stream, in particular V5 (Zeki, 1978; Newsome and Pare, 1988). Poor colour responses would be expected on the basis of weak input to ventral pathways (Yukie and Iwai, 1981) and fewer than normal P-type projections following V1 lesion (Cowey *et al.*, 1989). The lack of high-resolution receptive field properties in the superior colliculus (Goldberg and Wurtz, 1972) and prestriate areas (Zeki, 1993) is also consistent with the severely affected spatial responses in patients.

Although the performance achieved by humans and monkeys is consistent with the known anatomical projections and neural substrates that remain in the absence of V1, there remains an intriguing paradox. Hemianopic patients insist that they do not see the stimuli they are able to discriminate in their hemianopic fields. Two response modes have been defined subsequently. The first describes visual discriminations made in the absence of any awareness of the visual stimulus, a condition originally dubbed 'blindsight' (Weiskrantz *et al.*, 1974) and more recently described as 'agnosopsia' (Zeki and ffytche, 1998). The other mode, known as residual vision and more recently named 'blindsight type 2' (Weiskrantz, 1998) or 'gnosopsia' (Zeki and ffytche, 1998), refers to visual discriminations made when the subject is aware of the stimulus. Even when aware, patients insist that they do not see, and it is this striking qualitative difference that we investigate here.

Methods

Subjects

Patient GY (42 years of age) was rendered hemianopic by a lesion to the left occipital lobe sustained at age 8 years. The occipital pole in the left hemisphere has remained intact and is consistent with the macular sparing observed in his visual fields (Barbur *et al.*, 1980). The lesion extends ventrally to the lingual, but not fusiform gyrus, dorsally to the cuneus and part of the precuneus, and anteriorly to the occipitoparietal sulcus (Brent *et al.*, 1994). On the basis of these anatomical structures, the lesion is thought to include all of V1 and perhaps some of V2. There is also a small lesion to the parietal lobe of the right hemisphere (Brent *et al.*, 1994). This lesion has not been shown to have any effect on the visual tests applied in the left hemifield, which has exhibited normal visual responsiveness in studies conducted in this laboratory. GY is a very experienced psychophysical observer who has been tested in many laboratories over a period of 20 years. His residual visual responses to spatial structure are grossly impaired (Barbur *et el.*, 1980) and his colour responses are poor (Brent *et al.*, 1994), but effectively normal responses to fast motion have been observed (Blythe *et al.*, 1986). All responses described above were obtained when GY was aware of the visual stimulus.

We also tested three healthy control subjects, ABM, ALF and ED, all authors of this paper. All control subjects had normal uncorrected visual acuity, colour vision and visual fields. Informed consent was obtained from GY and the control subjects for the experiments described in this paper, which were approved by the human ethics committee of Imperial College, London.

Visual stimuli

All visual stimuli were generated with a four-channel Maxwellian view optical instrument (Barbur *et al.*, 1980). The light stimulus comprised three elements: two drifting gratings and a spatially uniform background field. The gratings were 10° in diameter, vertically orientated, and drifted from right to left. The background field extended over a circular region of diameter 49° and had a small (0.1°) circular fixation spot at its centre. Within the background field, two circular field stops were positioned such that they were spatially coincident with the drifting gratings. This

arrangement produced drifting gratings of high, constant (>90%) contrast surrounded by an independent background field.

Maxwellian view overcomes light-scatter problems associated with free viewing of a light-scattering screen such as a VDU. There remain other sources of scatter, for example within the ocular media and internal reflections from the retinal layers or sclera. We arranged our stimulus with the background field, which is of sufficient brightness (3.0 log trolands) to make these factors implausible sources of light-activated responses from GY's hemianopic field.

Our aim was to investigate the ability of an observer to match or discriminate between the two gratings on the basis of velocity, luminance or chromaticity. We required, therefore, one of the gratings to be continuously variable in velocity, luminance and chromaticity, whilst the other could be held fixed within any trial. The stimulus attributes were manipulated in the following manner.

Rotating large, square-waveform, radial gratings in the back focal planes of the instrument's optical channels generated grating motion. The motion was, therefore, quasi-linear. The gratings were rotated by means of precision DC (direct current) servomotors and low ratio gearboxes. The speed of the rotation was varied by means of an accurate 10-turn potentiometer, which could be controlled by the observer. Continuous variation of the stimulus luminance, but not contrast, was effected by the use of a fixed Polaroid filter and a Polaroid analyser, which could be rotated by the observer. Fixed, reference values of grating luminance were generated by the appropriate selection of calibrated neutral density filters. In order to generate continuous variation in chromaticity along the spectrum locus beyond 545 nm, we employed interference filters to produce two narrow-bandwidth spectral stimuli of wavelength 545 and 656 nm. The interference filters were placed in separate channels of the Maxwellian view system. The two light channels were polarized orthogonally by fixed Polaroid filters. Following recombination of these channels, a single rotatable Polaroid filter provided continuous variation of the mixture of the quasi-monochromatic primaries. The recombination of the spectral stimuli occurred before the grating stimulus, thereby generating a single drifting grating of variable chromaticity. We also examined the blue–green region of the spectrum locus by using primary stimuli of wavelengths 453 and 514 nm. Fixed, reference values of grating chromaticity were generated by using other interference filters. In addition to the spectral colour matching, a dichromatic mixture of 600 and 470 nm primaries was matched to a white stimulus (colour temperature ~3000 K). When required, stimulus duration was controlled with electromechanical shutters. We employed two principal stimulus configurations for each of the stimulus attributes we investigated. In one, the gratings were positioned in opposing hemifields. The stimuli were both 10° above fixation, with one 10° left and the other 10° right of fixation. The other configuration comprised the same gratings, but they were presented to the right hemifield alone. The gratings were both 10° right of fixation, but one was 10° above and the other 10° below fixation.

Calibrations of the luminance, duration and speed, and spatial extent of all visual stimuli were performed *in situ* with the use of a photometer, oscilloscope and travelling microscope respectively.

Protocols

For each of the stimulus variables tested, namely motion, luminance and chromaticity, we employed two protocols. The first, a matching procedure, required the subject to set the test stimulus attribute to a value that matched a constant reference stimulus. The observer was presented with one grating of fixed velocity, luminance and chromaticity, and made adjustments to a single attribute of the other grating. The adjustments were made during continuous viewing of the stimulus. Throughout we employed drifting gratings because they induced a stable percept in GY's blind field, such that only his stimulus manipulations caused a change in his perception. For each reference value, the subject made 10 adjustments of the test grating. For all matches, GY was instructed to maintain fixation and not look at the stimulus presented in his right, hemianopic field at any time. Although the majority of measurements were made without assessment of eye movements, we performed two selected matching experiments while eye position was recorded with DC electro-oculography.

Our second protocol comprised a forced-choice discrimination task. In these tests, the reference grating was again fixed in velocity, luminance and chromaticity, but the test grating attribute was set at random to one of five possible values. Ten presentations were made, each of 1 s, at each of the five test stimuli. The subject was instructed to use the responses of 'brighter' or 'dimmer' to describe the test stimulus relative to the reference stimulus when luminance was manipulated. For velocity manipulations, responses of 'faster' or 'slower' were used. When chromaticity was varied along the spectrum locus beyond 545 nm, we required a response of 'redder' or 'greener' from the subject.

All measurements were preceded by 5 min of dark adaptation to allow significant cone but not rod adaptation. Subjects were then able to adapt rapidly to the uniform background field before measurements commenced.

Analysis

The psychometric functions derived from our forced choice experiments were analysed in order to obtain a measure of the subjects' discrimination performance. We used least-squares minimization to fit Boltzmann functions to subject response data. The change in parameter, e.g. luminance, required to increment performance from chance (50%) to 73% was used to represent the discrimination performance.

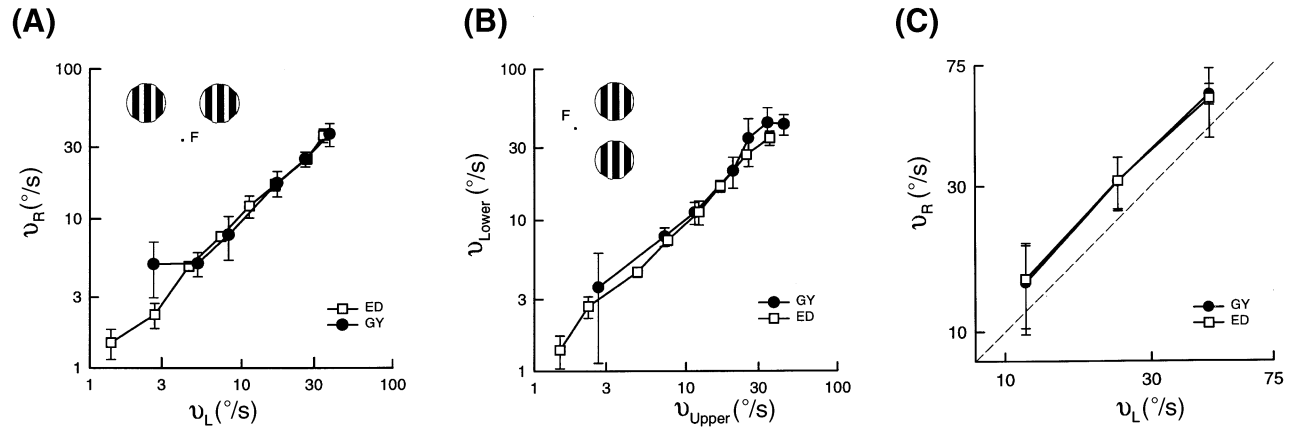

Fig. 1 Velocity matches established by GY (filled circles) and control observer ED (open squares) for 10°, circular, vertically orientated gratings of periodicity 0.2 cycles/° and mean luminance 2.7 log trolands drifting from right to left (see schematic). (**A**) Matches made to reference speeds presented to the left hemifield (υ_L) by manipulation of the test speed of the right hemifield stimulus (υ_R). (**B**) GY and ED's matches made in the right hemifield. Adjustments were made to the speed of the lower right stimulus (υ_{Lower}) to match the speed of the upper right stimulus (υ_{Upper}). (**C**) As for **A**, but the spatial frequency of the grating in the right hemifield was half (0.1 cycles/°) that of the stimulus presented to the left hemifield (0.2 cycles/°). In all panels, error bars represent the standard deviation of the mean of 10 matches. Data are plotted on common logarithmic scales. F marks the small circular fixation spot.

Results

Motion

Velocity matches

Adjustments to the right field stimulus speed are plotted as a function of the left field reference speed in Fig. 1A. GY was able to make perfect speed matches, over a range of reference speeds between 5 and 30°/s. GY's matches were, therefore, entirely consistent with those of the normal observer, ED, over this range of speeds. Below reference speeds of 5°/s, however, GY adjusted the right field stimulus to an abnormally high speed. With the forced choice detection task, we determined that the right field stimulus was not detected (with awareness) by GY at speeds of <5°/s. Thus, GY set the test grating speed at the limit for stimulus detection for reference speeds of <5°/s. We repeated the speed-matching experiment with the same gratings presented in the hemianopic field. The data plot in Fig. 1B demonstrates that GY was capable of matching speed within his hemianopic field, again, for speeds of >5°/s. At speeds below this limit, GY's matches had very high errors, although the mean of the adjustments appeared veridical.

Although the experiments described above suggest that GY was able to make matches on the basis of stimulus speed, temporal frequency encoding could also have mediated the responses. To evaluate the effect of temporal frequency, we repeated the experiment shown in Fig. 1A but replaced the right field grating with one that had half the spatial frequency. The matches established with this stimulus configuration are plotted in Fig. 1C. For GY and the control (ED), settings of the right field stimulus speed were consistently higher for the coarser grating, the data falling on a line of unit gradient but displaced by a fixed offset. This offset indicates that both GY and ED perceived the right-hand grating as moving more slowly by a factor of 1.22 than the left-hand grating of twice the spatial frequency. A value of 2 would be predicted if the matches were made on the basis of temporal frequency alone. Both subjects, therefore, did not make matches on the basis of temporal frequency alone. It should also be noted that this experiment also shows that auditory cues from the servomotors did not mediate matches. If that had been the case, GY's matches would not have changed as a result of the manipulation of grating spatial frequency.

Velocity discrimination

In addition to the investigation of speed, we also applied a test of direction discrimination between the moving gratings, in order to confirm that GY processed velocity as opposed to speed. In this test the subject was required to report the direction of motion as leftward or rightward for 10 randomly selected, 1 s presentations of each direction at test speeds of 10, 20 and 30°/s. GY was able to discriminate leftward from rightward motion with 100% accuracy for five presentations of each direction at each speed. This allowed us to conclude that GY's matches were made on the basis of velocity. These experiments were conducted while GY was wearing earphones through which music was played at sufficient volume to mask the servomotor noise.

In the light of having demonstrated what appeared to be entirely normal visual responses to motion, we wanted to examine GY's performance further. We measured forced choice velocity discriminations for stimuli presented simultaneously, for a duration of 1 s, in opposing hemifields. The probability of GY and a control observer responding 'faster' is plotted as a function of fractional change in the test velocity for a series of three reference velocities in Fig. 2A and B, respectively. The data plots illustrate that GY was able to discriminate between the stimuli, although the slopes of his psychometric functions were shallower than those of

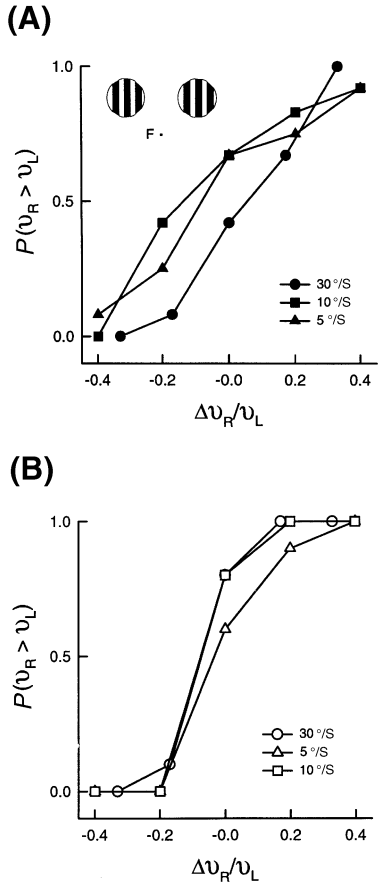

Fig. 2 The probability of the right hemifield stimulus being perceived to move faster than the left, plotted as a function of fractional change in test velocity. Data are given for reference velocities of 5, 10 and 30°/s, represented by triangles, squares and circles, respectively. Responses derived from GY and a control (ED) are shown in panels **A** and **B**, respectively. The circular gratings drifted from right to left and were 2.7 log trolands and of spatial periodicity 0.2 cycles/°.

the normal subject. In addition, for both GY and the control, the psychometric functions collapsed onto a single curve. This feature indicates that both observers' responses conform to Weber's law.

The psychometric functions shown in Fig. 2 were analysed in order to derive discrimination thresholds, which are presented in Table 1. GY's thresholds were divided by those of the normal subject, such that they are expressed in multiples of the normal threshold. For stimuli presented in the left and right hemifields, GY's thresholds were between 2 and 3 times those of the normal subject, with the largest threshold at the slowest speed, 5°/s (Table 1). The velocity discrimination threshold for stimuli presented to the hemianopic field alone was 3.6 times larger than normal and was therefore larger than any determined for stimuli presented to opposing hemifields (Table 1). GY had entirely normal velocity discrimination thresholds in the normal field (1.1 ± 0.1 times normal).

Table 1 *Performance achieved by GY during discrimination of test stimuli from reference stimuli*

Reference stimulus	Right hemifield	Left versus right hemifield
Motion		
5°/s	–	2.9 ± 0.6
10°/s	–	2.8 ± 0.7
20°/s	3.6 ± 0.8	2.0 ± 0.4
Luminance		
3.0 log troland (20°/s)	3.0 ± 1.0	2.8 ± 0.8
Colour		
600 nm (20°/s)	3.5 ± 0.6	2.5 ± 0.6

The reference stimuli are described in the left-hand column. The two right-hand columns denote performance obtained for stimuli presented in the right, blind hemifield alone, and when stimuli were in opposing hemifields, respectively. Data are given as multiples of the incremental step discriminated by normal controls. Errors indicate the 95% confidence interval of the results.

Summary

Stimulus motion above speeds of 5°/s appeared to be perceived equivalently in the two hemifields. There was, therefore, an explicit representation of visual motion derived from the hemianopic field which mapped directly onto normal motion perception. However, the encoding of motion in the hemianopic field was ~2–3 times less accurate than normal (Table 1).

Luminance

Luminance matching

GY made adjustments to the test grating luminance to match a series of reference grating luminances. The data obtained for stimuli presented in opposing hemifields are presented in Fig. 3A. The matches established by GY appeared to be unlawful. Increments in the reference luminance were not reflected by corresponding increments in the test stimulus. In contrast, the normal observer, ABM, made veridical matches, where the data fell on a line of unit gradient with zero offset. Our first concern was that we were not examining an appropriate range of reference and test luminances, so we evaluated GY's luminance detection threshold for the stimulus presented in his hemianopic field. The stimulus detection threshold (with awareness) is delimited by the shading in Fig. 3A.

Having established the detection threshold for the gratings, we conducted another matching experiment with the stimuli in the same spatial arrangement as that described above. We presented the reference stimulus to the hemianopic field and the test stimulus to the normal field. Thus, GY was required to make adjustments to the stimulus in the normal field to match a stimulus presented to the hemianopic field. We stimulated the hemianopic field with a grating of mean luminance 2.6 log troland. This was presented to GY on three separate occasions. The means of the 10 matches he

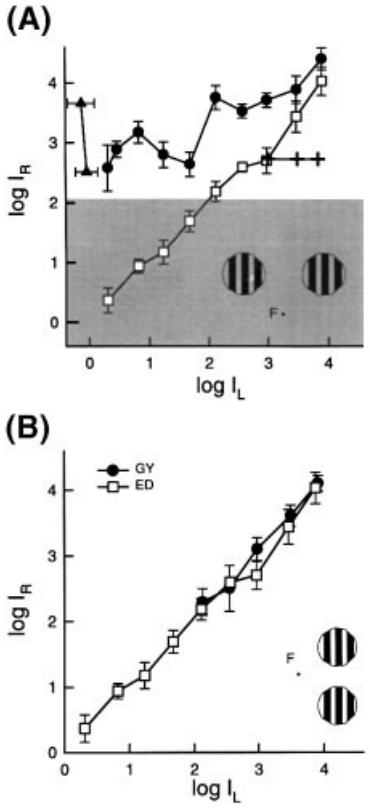

Fig. 3 (A) Luminance matches established with stimuli presented on either side of the vertical meridian. Adjustments of the right field stimulus luminance (I_R) are plotted against the left field reference stimulus luminance (I_L). Filled circles and open squares denote the data of GY and the control (ED), respectively. Adjustments made to the left field stimulus were also made by GY. Data obtained under these conditions are shown as crosses and triangles (see text for explanation). (**B**) As for **A**, but data were obtained for stimuli presented to the right hemifield alone. GY's matches are shown as filled circles and the data obtained from the control, as shown in **A**, are plotted for comparison as open squares. In both **A** and **B**, the circular gratings drifted from right to left at 20°/s and were of spatial periodicity 0.2 cycles/°. Error bars represent the SD of the mean of 10 matches in all cases.

made on each occasion are plotted in Fig. 3A as crosses. They clearly differ from the matches made when the stimuli were reciprocally arranged. In fact, GY made the stimulus in the normal field considerably brighter than the stimulus in the hemianopic field. When asked how he was making the matches, GY responded: 'If I am aware of something in my blind field, it must be bright, so I am estimating how bright I should make the match on the basis of my previous experience'. The previous experience to which he refers does not give him reliable information concerning the brightness of the stimulus. On each of the three occasions on which we applied the test, the 10 matches formed significantly different distributions when analysed using Student's t test ($P_{1,2} = 0.05$, $P_{1,3} < 0.00001$, $P_{2,3} < 0.002$, where the subscript denotes the occasions of testing). He could not, therefore, accurately replicate his matches on three separate occasions. Following his comments, we asked him not to use this method of estimation, but to simply make the stimulus in his normal field neither brighter nor dimmer than the stimulus in the hemianopic field. We tested GY with two reference stimuli in the hemianopic field, one at 2.5 log trolands and another at 3.7 log trolands. The means of 10 matches made to each of these stimuli are plotted in Fig. 3A as triangles. Again, these matches appeared inconsistent with previous matches. Moreover, the log unit increment in the reference luminance was not reflected in the adjustments to the test stimulus, which were negligible.

The results described above could have resulted from an absence of luminance-modulated responses within the hemianopic field. To investigate this possibility, we changed the stimulus arrangement such that the two gratings were presented in the hemianopic field. We repeated the matching experiment, and found that, just as a normal observer, GY established matches that fell on a line of unit gradient with zero offset (Fig. 3B). Moreover, GY's responses were well behaved and linear at luminance values approaching his threshold. We demonstrate, therefore, that GY has accurate luminance encoding derived from his hemianopic field. This result does not provide an adequate explanation of the response pattern seen in the interhemifield matches.

Luminance discriminations

At this stage the results seemed confusing. GY was able to make matches on the basis of luminance when stimuli were presented in the hemianopic field, but failed to use that luminance encoding when establishing matches between stimuli presented to opposing hemifields. In order to investigate this perplexing issue, we conducted three forced choice discrimination experiments in which we used different luminance ranges for the test stimuli, but in each case the reference luminance was fixed at a single value of 3.1 log troland. GY's results are plotted in Fig. 4A, which shows three psychometric functions of broadly similar properties. Each function reflects a low probability of a 'brighter' response at low values of each luminance range and a high probability at high values of each luminance range. In contrast, when we applied the same test in GY's hemianopic field alone, his data for the three different luminance ranges fell on a single function (Fig. 4B). This feature was also found in the data of a control observer, ABM (Fig. 4C). It appears, therefore, that GY displayed a normal response when stimuli were restricted to his hemianopic field, but when he was required to compare stimuli in opposing hemifields the percept derived from the right field stimulus luminance was not anchored to the percept derived from the normal hemifield. In Fig. 4D, the luminance ($I_{0.5}$) at which GY responded with 50% 'brighter' responses (Fig. 4A) is plotted against the central value (I_C) of each test luminance range. The plot clearly shows that GY was equating the central luminance value as equivalent to the luminance he was presented with in his left, normal hemifield. The data suggest, therefore, that GY was arbitrarily assigning the central luminance value as equal to the reference luminance. This

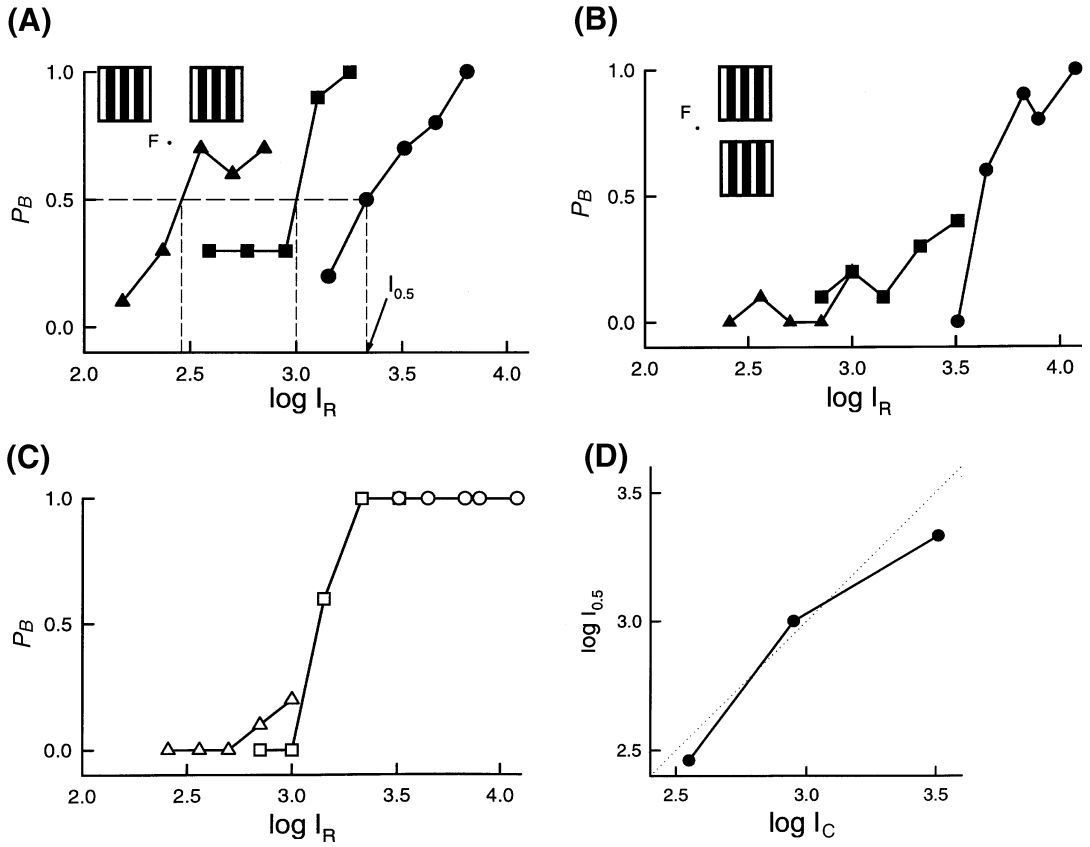

Fig. 4 (**A**) The probability of the stimulus in the right field being perceived as brighter than the stimulus in the left field (P_B), plotted against the right field test stimulus luminance (I_R). Data were obtained for three ranges of test luminances, but the same left field reference luminance of 3.1 log troland was used in each case. Data for lower, mean and brighter ranges are denoted by triangles, squares and circles, respectively. A value of luminance ($I_{0.5}$) for $P = 0.5$ is derived, as shown by the broken construction lines, for each psychometric function. (**B**) As for **A**, but data are given for a stimuli presented exclusively to the right hemifield. Data are given for observer GY. (**C**) As for **B**, but data are given for control observer ABM. (**D**) $I_{0.5}$, as derived from **A**, plotted as a function of the central value of each test luminance range (I_c). Data are given for GY (filled circles), and a broken line represents the line of unity. In all cases the gratings were of spatial periodicity 0.2 cycles/°, drifted from right to left at 20°/s and occupied a square region of 10 × 10°.

effect was obtained following the lengthy set of matching experiments and therefore indicates that continued exposure to the task did not allow GY to calibrate the luminance-modulated percept derived from the right hemifield with normal brightness perception.

We also analysed the psychometric functions in order to derive a measure of luminance discrimination threshold, as described previously. Thresholds for luminance discrimination were 2.8 and 3.0 times that of the normal for stimuli in opposing hemifields and the hemianopic field alone (Table 1).

Summary

On the basis of the experiments described above (Figs 3 and 4), we conclude that the luminance-modulated percept derived from the hemianopic field is not mapped to a perceptual dimension that can be compared with normal brightness perception. The two percepts seem to be unrelated and uncoupled. Luminance discrimination thresholds in GY are also considerably elevated.

Colour

Colour matches

For the investigations of colour, we measured matches established both in opposing hemifields and within the hemianopic field alone. Colour matches were quantified as the common logarithm of the ratio of the photopic luminances of the spectral primaries of the test stimulus. This parameter is plotted as a function of the reference stimulus wavelength λ. For reference wavelengths beyond 546 nm, GY's matches for stimuli falling in opposite hemifields were effectively identical to those made by the control subject, ABM (Fig. 5A). Figure 5A shows a plot of the match established by GY when he manipulated the stimulus in his left hemifield to match the reference stimulus, which was presented to the hemianopic field (filled triangle). Again, the match was consistent with that of the normal subject. In addition, when both reference and test stimuli fell in the blind hemifield, GY's matches appeared normal (Fig. 5B). GY was asked how he achieved his interhemifield red–green matches. In response, he said 'I make the stimulus neither too red nor too green compared to the stimulus in the normal field'. He

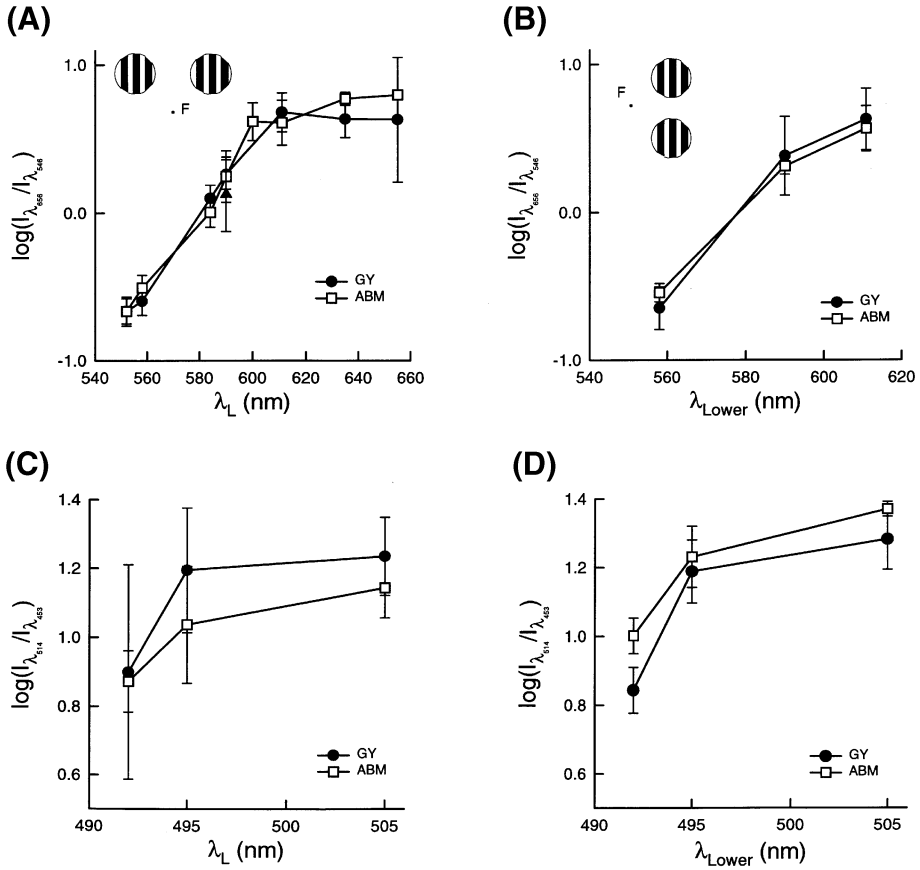

Fig. 5 Colour matches established by GY and ABM are denoted by filled circles and open squares, respectively. Data are plotted in terms of the ratio of spectral primaries ($I_{\lambda 656}/I_{\lambda 546}$) required to match the reference wavelengths (λ). The mean of 10 matches is plotted, and error bars denote the standard deviations of these values. (**A**) Matches made for reference wavelengths (λ) between 546 and 656 nm. Stimuli were presented to opposite hemifields and adjustments were made to the right hemifield stimulus. (**B**) As **A**, but in this case stimuli were presented to the right hemifield alone. (**C**) As **A**, but matches were made for reference wavelengths (λ) between 454 and 514 nm. (**D**) As **C**, but for stimuli presented to the right hemifield alone. All colour matches were made for circular gratings of spatial periodicity 0.2 cycles/° drifting at 20°/s and having mean illuminance 2.7 log troland.

was then asked if it was the same as normal red or green. He responded by saying 'Nothing is the same; I just know I can do this match'. GY's comments on the colour matches therefore differed from his comments on his luminance matches. For luminance he indicated that he was trying to make judgements based on his experience, whereas for colour he indicated he was making a comparison.

To test 'blue–green' colour processing, we used spectral primaries at 514 and 454 nm, between which wavelengths tritanopes (observers with an absence of short-wavelength-sensitive cones) have very poor discrimination. Normal wavelength discrimination in this region of the spectrum is, therefore, mediated by short-wavelength-sensitive cone pathways. The data plotted in Fig. 5C show that GY's matches were normal for reference wavelengths between 454 and 514 nm when the reference and test gratings were in opposing hemifields. The same was true for matches made for stimuli presented in GY's hemianopic field (Fig. 5D).

In addition to the spectral colour matches, we also provided a dichromatic mixture of 470 and 600 nm to match a non-spectral white stimulus. GY mixed the primary stimuli in the same proportion as the normal subject (ABM) within the limits of error ($P > 0.2$).

Colour discrimination

We examined colour discrimination in the red–green region of the spectrum. Initially, we measured responses when the reference and test stimuli were in opposing hemifields. Using a procedure similar to that adopted to test luminance discrimination, we chose three ranges of chromaticity over which the five test stimuli were selected. Subjects discriminated test stimuli from a reference stimulus of 600 nm wavelength. GY's responses and those of a normal control, ABM, are plotted in Fig. 6A and B, respectively. The three psychometric functions of each observer fell on a single function, a feature not observed in GY's responses to luminance variations (Fig. 4A). In this instance, therefore, GY's responses accurately reflected the manipulations of the physical stimulus. The main difference between the two observers was in the steepness of their psychometric functions, which when analysed showed that GY was 2.5 times worse than normal at this chromatic

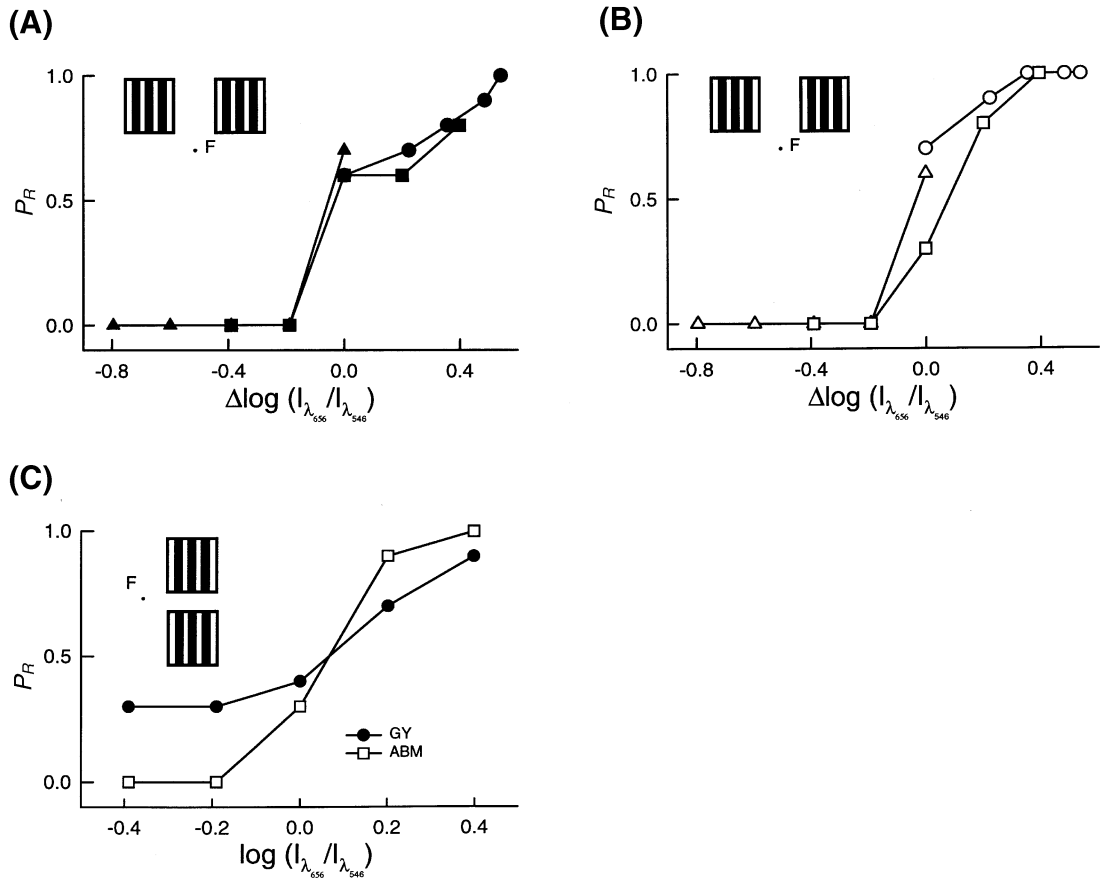

Fig. 6 The probability of the right field stimulus being perceived as redder than the left field stimulus (P_R) for square gratings of spatial periodicity 0.2 cycles/° drifting at 20°/s and of mean illuminance 2.7 log troland. Data are given for three colour ranges in ascending order of redness, denoted by the triangles, squares and circles, respectively. The reference stimulus presented to the left hemifield was a pseudomonochromatic (600 nm) orange. Data for GY and control observer ABM are given in **A** and **B**, respectively. (**C**) As for **A** and **B**, but for stimuli presented to the right hemifield alone. Filled circles and open squares denote data for GY and ABM, respectively, for a single range of test stimuli.

discrimination (Table 1). We also measured GY's discrimination for stimuli presented to the hemianopic field alone. These data were obtained for a single set of test stimuli. The responses are plotted in Fig. 6C, and illustrate that GY's discrimination for stimuli within his hemianopic field was 3.5 times worse than normal (Table 1).

Summary

GY's colour matches appeared entirely veridical for stimuli presented in opposing hemifields, and also when presented in the hemianopic field alone. GY was, however, worse than a normal at colour discrimination (Table 1).

Interactions

The results described above are for manipulations of single stimulus attributes. The results described below concern the interactions between stimulus attributes and thus can be used to evaluate the potential influence on the perception of one attribute contingent on variations of another.

Velocity and luminance

There is a dependence of perceived speed on the contrast of the visual stimulus in normal subjects (Thompson, 1982). Such a dependence could have allowed GY to encode luminance on the basis of perceived speed. For the purpose of this study we examined speed matches for a series of different luminances and contrasts. In Fig. 7A the speed of the test stimulus is plotted as a function of its luminance. For both GY and the control, the matches did not vary over a large range of luminance. Thus, neither subject would be capable of establishing luminance matches on the basis of perceived speed. When we varied grating contrast, the perceived speed increased for a normal subject at very low contrasts (Fig. 7B). However, the grating was not detected by GY at such low contrasts (Fig. 7B). Our measurements demonstrate, therefore, that the luminance matches made by GY could not have been achieved on the basis of a change in perceived speed.

Colour and luminance

Small changes in the overall luminance of the dichromatic colour mixtures in the test stimulus are probably unavoidable.

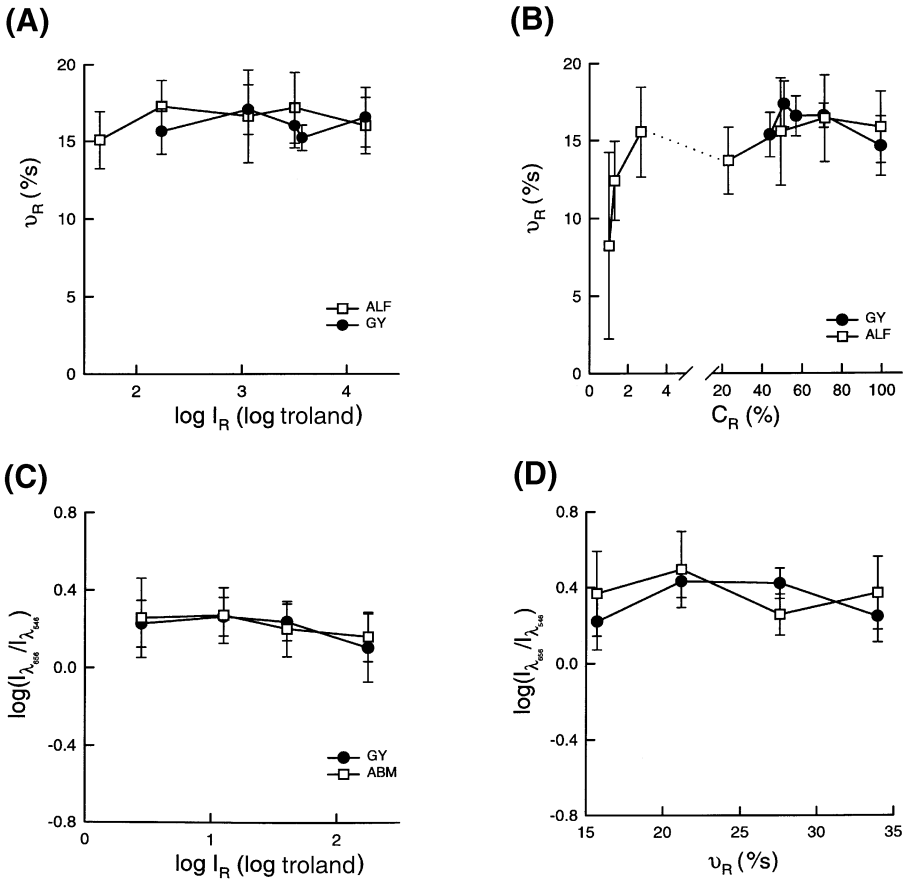

Fig. 7 (**A**) Velocity matches, established for stimuli presented to the left and right hemifields, plotted as a function of the right field stimulus luminance (I_R). The left hemifield stimulus was at constant luminance and speed of 2.75 log troland and 18°/s, respectively. (**B**) Velocity matches made for the same stimulus arrangement as in **A**, plotted against the right field stimulus contrast (C_R). (**C**) Colour matches made for different values of the left field luminance. The reference wavelength was 600 nm. (**D**) Colour matches made for different values of the right field stimulus velocity. In all panels adjustments were made to the right field stimulus, and filled circles and open squares denote the matches made by GY and the control, respectively. All gratings were circular and were of spatial periodicity 0.2 cycles/°.

Although unlikely, particularly in the light of his own inability to use luminance to establish matches, a luminance cue could have provided GY with a signal with which he could match colours. In order to address this potential cue, we measured colour matches over a range of different reference luminances. The data, plotted in Fig. 7C, reveal that the colour matches were invariant with respect to the stimulus luminance for both GY and the normal control, ABM. As the colour matches remained stable over a large range of variation of stimulus luminance, chromatic- and not luminance-modulated responses must have mediated the responses.

Colour and velocity

We measured dichromatic colour matches at a series of speeds of a 600 nm reference grating. The colour matching data are plotted as a function of speed in Fig. 7D. Within the accuracy of our measurements, the colour matches made by GY appeared independent of grating speed. It is implausible that the colour matches made by GY were established on the basis of perceptual variations in speed resulting from colour changes.

Interhemifield interactions

A recent study (Finlay *et al.*, 1997) has shown that moving stimuli presented to GY's normal hemifield can induce a motion percept in the blind hemifield. Such an effect may interfere with matches made between stimuli presented to the two hemifields. Our stimuli were designed to minimize any such effects. The stimuli here were smaller, and in a direction of motion opposite to those which Finlay and colleagues found to be most effective (Finlay *et al.*, 1997). GY was also questioned about such a transferred percept, and he responded that he perceived nothing in the blind field on stimulation of the normal field alone.

Fixation

GY has been shown to have very steady fixation (Barbur *et al.*, 1993). In our experiments GY was acutely aware if an involuntary eye movement caused visual stimuli to fall within his normal field. As in previous experiments (Finlay *et al.*, 1997), GY reported such events. In these circumstances all matches measured at the relevant reference value were discarded and another reference value was selected. Our procedure was designed to prevent GY from obtaining any feedback from information derived from his normal visual field. In practice, we had to follow this procedure on only four occasions.

We also measured eye movements during colour and motion matches of stimuli presented in the opposing hemifields. GY first fixated the fixation point and was then required to fixate two eccentric points 5° and 15° to the left of fixation, and then return to the central fixation in reverse sequence. During this period the experimenter changed the motion or colour of the stimulus in the blind hemifield. GY was then instructed to maintain fixation and make adjustments to the speed or colour of the blind field stimulus. Once the match was established, GY was instructed to repeat the initial calibration sequence of eye movements. In 10 trials GY matched a 12°/s reference speed with a mean adjustment of 13.0 $\pm$ 1.0°/s. In the case of colour, a 584 nm reference was matched with a mean of 10 adjustments of effective wavelength 582 $\pm$ 10 nm. During all trials, which lasted ~25 s, GY held steady fixation, as indicated by the absence of any fast phase eye movements other than those generated in the calibration sequences. GY was capable, therefore, of achieving matches of motion and colour whilst maintaining central fixation.

Discussion

We have investigated the visual function referred to as blindsight type 2 by Weiskrantz (Weiskrantz, 1998) and as gnosopsia by Zeki and ffytche (Zeki and ffytche, 1998) by using a matching procedure. We assert that if an observer is capable of voluntarily manipulating a stimulus parameter such that he can establish lawful (but not necessarily veridical) matches, he possesses a conscious representation of the stimulus parameter. Although the principal goal of this study was to determine the relationship between the percepts derived from the normal and hemianopic fields in GY, the data derived from the blind hemifield alone merit discussion with respect to other psychophysical studies of vision in the absence of V1.

When two drifting gratings were presented to GY's hemianopic field, he was capable of making veridical matches on the basis of velocity, luminance and chromaticity. Matches made on the basis of stimulus motion were normal above 5°/s. Another study (Weiskrantz *et al.*, 1995) found that GY perceived stimuli above this speed with awareness. GY is incapable, therefore, of establishing velocity matches when he is unaware of the stimulus. This finding is consistent with our assertion that lawful matches can only be established when the observer is aware of the stimulus. Our data show that GY finds discrimination between the speed of drifting gratings more difficult than discrimination between single moving dots (Barbur *et al.*, 1980) or apparent motion (Blythe *et al.*, 1986). This could be a result of the lack of a displacement cue in the drifting grating stimuli, a feature present in presentations of apparent motion and a single moving dot. GY's veridical luminance matches demonstrate that he had conscious access to luminance modulations in his blind field, although he was significantly poorer than normal at luminance discriminations (Table 1). Colour vision responses derived from the hemianopic field also demonstrate that GY had conscious and veridical access to chromatic manipulations of the stimulus. GY's chromatic discriminations were considerably worse than those of a normal subject (Table 1), but significantly better than those achieved by GY previously (Brent *et al*., 1994). Our results probably differ from those of Brent and colleagues because we used drifting gratings and not briefly flashed static stimuli. In addition, the retinal adaptation with a 3 log troland background employed here is probably sufficient to remove any activity of rod receptors, which was suggested as the cause of much of the abnormality found in GY's spectral response and colour discriminations (Brent *et al.*, 1994).

We believe our measurements with stimuli presented to the hemianopic field alone demonstrate that GY had conscious access to motion, luminance and chromatic variations of the drifting gratings. However, GY maintains that he did not see our stimuli, i.e. there is a qualitative difference between the percepts he derived from the normal and hemianopic fields. This qualitative difference, described at length elsewhere (Weiskrantz, 1997), motivated our experiments that compared the percepts derived from the two hemifields, which are discussed below.

Motion perception

When stimuli were presented in opposing hemifields, GY made veridical matches on the basis of stimulus speed (not frequency). These matches were made at velocities the direction of which GY could accurately discriminate. So, in addition to his normal matches obtained from his hemianopic field, it also appears that GY perceived grating motion in the two hemifields as equal, at least above 5°/s. We believe, therefore, that GY is endowed with neural activity in the damaged hemisphere which in the normal hemisphere gives rise to normal motion perception. In the light of functional imaging studies on GY (Barbur *et al.*, 1993; Zeki and ffytche, 1998) and normal observers (Zeki *et al.*, 1991), V5 is a likely candidate for the neural correlate of conscious motion perception. It has also been demonstrated that the anatomical pathways that bypass V1 in the macaque can innervate neurons in V5 (Girard *et al.*, 1992). Further, studies of non-human primates have shown that behavioural responses to

motion can be modified by microstimulation of neurons in V5 (Salzman *et al.*, 1992) and long-lasting motion discrimination losses result from lesion of the same area (Pasternak and Merigan, 1994). In addition, a human patient with extensive bilateral lesions including human V5 has grossly abnormal motion perception, particularly for stimulus motions of >10°/s (Zihl *et al.*, 1983). It has also been reported that at speeds of >6°/s, activity in V5 is found to be elicited in advance of any that would be relayed via V1 (ffytche *et al.*, 1995). The conclusion of that study was that projections to V5 in the absence of V1 may be preferentially sensitive to fast motion. GY's responses are, therefore, consistent with previous studies on the characteristics of V5 and the projections to that area which survive lesion to V1. In addition, activity in V5 in the absence of activity in ipsilateral V1 endows GY with conscious perception of motion, as proposed previously (Zeki and ffytche, 1998). Moreover, the motion percept is equivalent to that derived from the normal hemifield, although less accurately encoded (Table 1).

Brightness perception

When the stimuli were arranged such that the matches were made between stimuli falling in the hemianopic and normal hemifields, GY was unable to establish a lawful set of luminance matches. This provides evidence that the luminance-modulated percepts derived from the hemianopic and normal hemifields are unrelated. That is, there is no unique mapping of the percept derived from the hemianopic field onto the perceptual dimension of brightness derived from the normal hemifield. By 'brightness' we mean the normal percept associated with luminance modulations. When GY had control of stimulus luminance in the normal hemifield he was unable to make matches that replicated those he established when he controlled the stimulus luminance in the hemianopic field. This demonstrates further the unrelated nature of the percepts derived from the opposing hemifields.

Discrimination experiments also confirmed the dissociation between the percepts derived from the opposing hemifields. GY's discriminations were based solely on the range of luminances presented to the hemianopic field, and there was no benefit derived from, or reference made to, the stimulus presented to the normal hemifield. Thus, the psychometric functions displayed similar response characteristics independent of the luminance values presented within each experiment. For GY, the luminance at which 50% of responses were 'brighter' was identical to the central value of the test luminance range (Fig. 4D). In one instance, therefore, GY appeared to respond such that the blind field was more sensitive than the normal hemifield. Such a result would not be predicted on the basis of a loss of sensitivity. This feature was also found when GY tried to estimate stimulus luminance in the hemianopic field and to use that estimate to match brightness.

Our interpretation of the results is that GY has a luminance-modulated percept derived from neural pathways that remain in the absence of V1. However, this percept is in no way comparable to the percept of brightness, which is derived from the normal visual field, and thus normal visual pathways, including V1. We conclude that V1 plays a crucial role in generating the normal percept of brightness. This hypothesis is supported by a recent electrophysiological study which showed that V1 neurons in cat accurately reflect perceived brightness (Rossi *et al.*, 1996).

The neural substrate encoding luminance in the damaged hemisphere has a number of potential sites. As reviewed in the introduction, both subcortical (Goldberg and Wurtz, 1972) and extrastriate cortical visual areas (Benevento and Yoshida, 1981; Yukie and Iwai, 1981; Cowey and Stoerig, 1989; Girard *et al.*, 1991, 1992) receive input in the absence of V1. Neurons in such areas are likely to provide the luminance encoding in GY's blind field. The responses to luminance in these alternative areas may be different from those found in V1. If conscious brightness perception could be derived from their output, however, a lawful, but not veridical, relationship between interhemifield luminance matches would result. The unlawful and arbitrary matches we observed indicate that visual areas surviving GY's lesion appear capable of providing a conscious representation of luminance, but do not endow GY with brightness perception derived from normal vision.

Colour perception

Dichromatic colour matches for stimuli in opposing hemifields show that GY had conscious access to chromaticity of stimuli presented to his hemianopic field. The measurements obtained for red–green modulations demonstrated that GY was able to match stimuli, which a subject lacking cones sensitive to medium or long wavelengths could not (Pitt, 1935; Wright, 1946). GY was also able to make matches at which a subject lacking short-wavelength-sensitive cones would be extremely poor (Wright, 1952). We have demonstrated, therefore, that GY has trichromatic input to colour mechanisms. Previous threshold measurements have revealed evidence of colour opponency and red- and green-sensitive cone mechanisms in GY (Brent *et al.*, 1994) and colour opponency in other hemianopes (Stoerig and Cowey, 1991).

Do our findings indicate that GY has a normal conscious percept of colour in his blind field? It appears that there must be some equivalence in the percepts of the chromaticity of the stimuli presented to the blind and normal hemifields. That is, a colour vision deficit would not be expected on the basis of GY's matches (Wright, 1946). On the basis of these data alone, GY appeared to have a normal percept of the colour of the stimulus with which he was presented.

As with other stimulus attributes, GY suffered a loss of colour discrimination (Table 1). However, when we employed offset ranges in our discrimination tasks, the procedure that highlighted the unrelated nature of percepts of luminance derived from opposing hemifields, GY showed entirely veridical responses. That is, his psychometric curves reduced

to a single function. The loss of colour discrimination GY suffers does not, therefore, lead to a dissociation in perception, and thus discrimination loss is unlikely to have done so in the case of luminance.

What are the likely candidates for the neural substrate of GY's colour perception derived from his hemianopic field? Colour-selective responses that exhibit colour constancy have been found in the cells of prestriate area V4 in the macaque (Zeki, 1980). In humans, lesion to the lingual and fusiform gyri can give rise to various colour vision deficiencies (Meadows, 1974; Zeki, 1990; Kennard *et al.*, 1995). That is, colour perception is disrupted such that colours no longer appear the same. Such deficits can also be restricted to one hemifield, in which case colours do not appear to match in the different hemifields (Kolmel, 1988). Activity in GY's inferior temporal lobe is, therefore, the most likely candidate for mediating his responses to colour. The sparser projections to the temporal lobe following V1 lesion (Cowey and Stoerig, 1989) may explain GY's poor discrimination of chromatic modulations, which could be further compromised by his lesion to the lingual gyrus, as proposed previously (Brent *et al.*, 1994).

A recent study has shown that V5 has access to chromatic modulations (Tootell *et al.*, 1995). Could activity in V5 or other areas outside the inferior temporal lobe give rise to the colour responses we observe in GY? Evidence provided by another patient study (Cavanagh *et al.*, 1998) showed that high colour-contrast, isoluminant, moving stimuli are accurately discriminated by patients with cortical lesions affecting colour vision. Perception of movement from colour is therefore possible in the absence of normal colour perception. This makes V5 and other areas outside the inferior temporal lobe unlikely candidates to mediate veridical colour matches even though they have access to chromatic signals encoding motion. An additional point made by Cavanagh and colleagues (Cavanagh *et al.*, 1998) was that V5 is unlikely to process motion from colour because of the poor chromatic contrast sensitivity found in V5 in the macaque, and it was suggested that the likely candidate for such processing in their patients is a putative dorsal representation of V4 (V4d).

It is also interesting to note that colour can be accurately matched in the absence of normal brightness perception. This is, in fact, the complementary dissociation to that found in achromatopsia, where responses to achromatic stimuli are spared but colour responses are degraded (Heywood *et al.*, 1987; Kennard *et al.*, 1995). The results of this study and those from studies on achromatopsia therefore suggest that chromatic information and brightness information to a great extent remain functionally segregated within the human brain.

Verbal comments

In this study, the subject was asked how he achieved his luminance and colour matches. In the case of luminance matching, GY's comments indicate that he was attempting to use previous experience, i.e. he was not using information that he could access 'on line'. In contrast, his comments concerning colour indicate that he was making an 'on-line' comparison and did not require previous experience. His statements appear to be consistent with the veridical and non-veridical interhemifield matches made on the basis of colour and luminance, respectively. When questioned about how colours appeared, however, GY indicated that no stimulus in his blind field was perceived as it would be if presented to the normal field. This is a confirmation of previously documented verbal commentaries given by GY (Weiskrantz, 1997), and is encapsulated in the definition of blindsight type 2 (Weiskrantz, 1998). The measurements we have made may not appear consistent with the lack of perceptual identity derived from the two hemifields. However, our operational approach revealed GY's specific loss of brightness perception, and we believe this is crucial to understanding why visual stimuli presented to his blind field are never, as a whole, perceptually equivalent to those presented to the normal field.

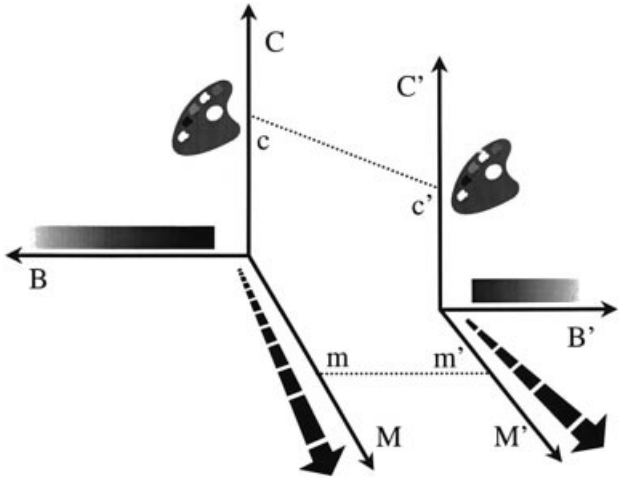

Fig. 8 A schematic representation of the perceptual spaces derived from the left, normal hemifield and the right, hemianopic field. See text for explanation.

Model of conscious vision

We propose that the percepts of colour and motion derived from the hemianopic field project uniquely onto the normal perceptual dimensions of colour and motion. However, GY's percept of luminance derived from his hemianopic field does not project uniquely onto the normal perceptual dimension of brightness. Within the hemianopic field, however, all matches were veridical. We propose the following framework within which GY's visual responses can be accounted for.

Firstly, we define normal visual perception in terms of three orthogonal perceptual dimensions, namely, colour, brightness and motion. By orthogonal we mean that variation along one dimension will not affect the value in any other dimension. As a first approximation, this is true of normal visual perception and for all our stimulus manipulations. Cartesian axes B, C and M, representing a framework of

normal visual perception, are illustrated in Fig. 8. A visual stimulus can be specified by its position in this perceptual space in terms of its motion, colour and brightness values. In GY, matches established in his hemianopic field were veridical and, therefore, a similar set of Cartesian axes, B′, C′ and M′, describe his conscious perception of luminance, colour and motion. How does GY's hemianopic perceptual space relate to the representation given for normal vision? We propose that the perceptual dimensions of colour and motion are parallel to the normal dimensions of these attributes, such that unique mappings between the percepts exist enabling matches between stimuli in opposing hemifields to be made. The lines cc′ and mm′ are examples of unique mappings of the stimulus attributes of colour and motion. In contrast, the unrelated nature of brightness matches between stimuli presented to opposing hemifields has led us to illustrate the two perceptual dimensions (B and B′) in opposite directions, such that they have no projection onto each other. We have also attempted to account for GY's thresholds for perception in the hemianopic field in our scheme. Elevation of the luminance and motion thresholds is reflected by a truncation and offset in the axes B′ and M′, respectively (Fig. 8).

We also believe that our model illustrates the principal reason why GY claimed not to see visual stimuli of which he was aware. The only assumptions that need be made are that brightness is the most fundamental of all visual attributes, and if a stimulus has no brightness it will not register as being visual. Our data have shown that GY does not possess a normal percept of brightness for stimuli presented in his hemianopic field, and our scheme suggests that this renders him blind. As such, GY's visual abilities derived from his hemianopic field remain self-consistent, but as a whole are unrelated to normal vision. It is, therefore, unsurprising that GY does not claim that a visual stimulus presented to his blind field shares perceptual identity with one presented to the normal field.

Conclusions

When stimuli were presented to the hemianopic field alone, GY was able to establish veridical matches on the basis of stimulus luminance, colour and motion. We conclude from this that GY has conscious access to variations in these stimulus parameters. When required to match stimuli presented in opposing hemifields, GY made veridical matches on the basis of colour and motion, but unlawful and arbitrary matches were made on the basis of luminance. We have demonstrated, therefore, associations between the percepts of colour and motion derived from the opposing hemifields, but a dissociation between the percepts associated with luminance modulations. We have presented a scheme that accounts for these results. In the light of the cortical lesion suffered by GY, data arising from other lesion studies in patients and the known properties of neurons and their projections in the visual system, we propose that conscious visual perception is organized in a modular manner consistent with previous proposals (e.g. Zeki, 1993). We conclude that the normal percept of brightness is represented in the primary visual cortex, or is crucially dependent on activity there, which subsequently projects to other areas. Colour perception results from neuronal activity outside V1, probably in those inferior aspects of the temporal lobe that could receive input following V1 lesion in GY. We also propose that motion perception arises from activity in V5, a conclusion supported by recent functional imaging studies (Zeki and ffytche, 1998). GY's case is, therefore, remarkably consistent with other lesion cases in which the perception of a single visual attribute is changed but others remain unchanged. We believe that GY's case is special, however, in that the loss of normal brightness perception renders him blind, i.e. he is aware of visual stimuli but is not visually aware. This final conclusion provides an explanation of blindsight type 2.

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Received September 21, 1998. Revised January 8, 1999.
Accepted January 29, 1999