Residual colour vision in a human hemianope: spectral responses and colour discrimination

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SUMMARY

We present data for a patient, GY, with a right hemianopia caused by traumatic damage to the left occipital cortex. Previous studies have established that this patient has residual vision which enables him to detect and localize transient stimuli presented to his ‘blind’ hemifield. We have now examined spectral responses associated with this residual vision by using two-colour incremental threshold methods to measure FI-spectral functions, and a white light background to examine spectral data for ‘colour-opponent’ characteristics. We report that both methods yield normal spectral response characteristics for GY’s ‘blind’ hemifield. We have also investigated the patient’s ability to identify, verbally, coloured stimuli presented to his ‘blind’ hemifield, and found that, in ‘forced choice’ experiments, he achieves a high proportion of correct responses to large stimuli. The patient reported that in threshold detection measurements his responses were based on the presence or absence of a percept associated with transient light stimulation of the ‘blind’ hemifield (residual vision), whereas colour naming was achieved without conscious perception of colour (‘blindsight’).

1. INTRODUCTION

Some patients with damage of the striate cortex are able to respond to certain classes of light stimuli presented within the ‘blind’ area of the visual field which projects to the damaged cortex. Such patients are able to localize transient stimuli by pointing with the hand, or by saccadic eye movements made to fixate the stimulus (Poppel et al. 1973; Weiskrantz et al. 1974; Perenin & Jeannerod 1975). These and other studies have demonstrated that patients may exhibit a variety of visual capacities in response to light stimulation of ‘blind’ areas of the visual field, including detection and velocity discrimination for moving stimuli (Barbur et al. 1980), discrimination of apparent (ϕ) motion (Blythe et al. 1986), discrimination of spatial orientation and resolution of spatial structure (Weiskrantz et al. 1974; Weiskrantz 1986), and wavelength discrimination (Stoerig 1987). Spectral sensitivity functions showing rod and cone influences have also been reported (Stoerig & Cowey 1989, 1991). In many instances, the patients experience no sensation in response to light stimulation of the ‘blind’ field, and visual sensitivity is revealed only by ‘forced choice’ techniques. This response mode was designated ‘blindsight’ by Weiskrantz et al. (1974). Other patients report that, in detection and localization of transient and moving stimuli, they perceive a ‘dark’ shadow located within the ‘blind’ region of the field, a response mode described as ‘residual vision’ (Barbur et al. 1980; Blythe et al. 1986). The retinal projection pathways which generate these response patterns have not been identified definitively, but it is frequently argued that many of the observed psychophysical responses are consistent with activity in visually driven neurons of the superior colliculus. An alternative explanation implicates the direct projections from the dorsal lateral geniculate nucleus (dLGN) to the pre-striate visual cortex (Benevento & Yoshida 1981; Fries 1981). In monkey, this projection survives ablation of the striate cortex (Yukie & Iwai 1981), and surviving ganglion cells project to the degenerated dLGN, where they contact, via an interneuron, surviving neurons which project to the pre-striate visual cortex (Kisvárday et al. 1991). A recent study using positron emission tomography (PET) has shown that presentation of moving stimuli to the ‘blind’ hemifield of a male hemianope, GY, activates pre-striate areas corresponding to V3 and V5 of the macaque, but not the striate cortex (Barbur et al. 1993). We have examined spectral responses and colour naming for stimuli presented to GY’s ‘blind’ hemifield. It has been shown that GY’s spectral sensitivity 30° off-axis in the ‘blind’ hemifield is scotopic in nature (Barbur et al. 1980), but we now demonstrate that spectral responses characteristic of red- and green-sensitive cone mechanisms and of post-receptoral ‘colour opponent’ mechanisms can be recorded for his ‘blind’ hemifield. We also establish that, with sufficiently large stimuli, GY can perform...
forced choice discrimination between different colours presented to his 'blind' hemifield.

2. METHODS

Spectral responses were determined by psychophysical methods which, in normal vision, yield data characteristic of either photoreceptor or of post-receptoral spectral organization. The two-colour increment threshold method (Stiles 1978) yields broad-band \( \Pi \)-spectral functions which are similar to the absorption and action spectra of the photopigments (Baylor et al. 1987). We determined \( \Pi \)-spectral responses by measuring threshold sensitivity for detection of a circular target (diameter 4.5°, duration 100 ms). The circular (17° diameter) background consisted of two components, one blue-green (515 nm) of fixed luminance (1.0 log trolands), which desensitized rod responses, and a second, of wavelength \( \mu \) and radiance \( P_{\mu} \), the latter being the variable in the measurements. A fixation spot allowed the target to be presented 10° off-axis, along the horizontal meridian. Initially, the target luminance at which it was just no longer detected against the 515 nm background was determined, but in subsequent measurements it was set 0.4 log units above this value. The \( \mu \) component was then added to the background, and its radiance, \( P_{\mu} \), adjusted until the target could again just no longer be detected. The radiance value \( (P_{\mu})_{o} \) at which this occurred was noted, and the procedure repeated for different values of \( \mu \), to give spectral sensitivities, \( S_{\mu} \), equal to \( (P_{\mu})^{-1} \). Data were obtained for target wavelengths 650 nm and 515 nm, which isolated the red-sensitive (\( \Pi_{R} \)) and green-sensitive (\( \Pi_{G} \)) responses, respectively. Spectral sensitivities were also recorded with a fixed, white background (luminance 1.4 log troland; colour temperature 3200 K), for which threshold radiance, \( (P_{\mu})_{n} \), was recorded as a function of the target wavelength \( \lambda \). In those with normal colour vision, spectral sensitivity functions recorded in this way exhibit features which are characteristic of 'colour opponent' responses associated with post-receptoral neural channels (Sperling & Harwerth 1971; King-Smith & Carden 1976).

All thresholds were measured by pressing one of two buttons, to denote either 'seen' or 'not seen' in response to presentation of a target. The parametric variable, namely the target radiance, \( P_{\mu} \), in 'colour opponent' response measurements, and the background radiance, \( P_{\mu} \), in \( \Pi \)-spectral measurements, was varied between presentations, under computer control. The radiance values were selected by a computer control, and that of the other two beams could be controlled to 0.1 log unit accuracy by neutral density filters. Narrow spectral bandwidths were obtained by placing interference filters (Balzer B40) in the collimated white light beams. The observer's eye position was centred relative to the 3 mm exit pupil of the instrument, and maintained by the observer's biting on a dental clamp. Radiometric and photometric calibrations were performed with a Macam Photometer/Radiometer.

(b) Procedures

All experiments were preceded by 15 min of dark adaptation, and were performed in a dark room. In colour-naming experiments, the observer initially examined each of the three test stimuli under foveal presentation, to select its colour description (e.g. 'red' for 665 nm). During the experiment, the observer identified each stimulus, presented non-foveally, by using one of the descriptions (e.g. red, green or blue) given to the three test stimuli seen under foveal fixation. Unless otherwise stated, all measurements were made with the right eye, the nasal retina of which projects to GY's damaged hemisphere.

(c) Observers

GY, a 36-year-old male, has a hemianopic field loss, caused by traumatic damage to the left striate and pre-striate cortical area, incurred in a traffic accident when he was 8 years old. A magnetic resonance image (MRI) scan, similar to that for GY published by Barbur et al. (1993), revealed an extensive lesion in the left hemisphere, which involves the lingual gyrus, the striate and peristriate cortex below the calcarine fissure to within about 1 cm of the occipital pole, and the similar cortex above the calcarine fissure, not quite extending to the occipital pole. The fusiform gyrus is spared. The medial aspects of the cuneus, to the sulcus parieto-occipitalis anteriorly, a small strip of the posterior aspect of the pre-cuneus in the parietal lobe, and the caudal extremity of the parahippocampal gyrus are also involved. A much less extensive lesion on the right side involves the cortex of the right, mainly inferior parietal lobule, part of the supramarginal gyrus and juxta cortical white matter of the adjacent part of the superior parietal lobule. Much of the geniculo-calcarine tract is involved on the left but not on the right side, and no abnormal visual functions resulting from the right-sided lesion were observed. A detailed visual field plot showed a right hemianoptic loss, with sparing of sensitivity extending up 3.5° to the right of the fixation point (Barbur et al. 1980). Visual responses for GY's left hemifield have normal increment threshold sensitivity, and normal colour vision as assessed by the Ishihara pseudo-isochromatic plates and by colour matching. Control data are given for GY's left hemifield, and for two controls with normal colour vision, PB and ML, both males, aged 26 years and 43 years, respectively. All three observers were experienced in psychophysical measurements.

3. RESULTS

\( \Pi \)-spectral response data measured under conditions which should isolate the long-wavelength sensitive, \( \Pi_{S} \) mechanism are plotted in figure 1a. For wavelengths

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Figure 1. Relative spectral sensitivity, $S_\lambda$, plotted against wavelength, $\lambda$. The 4.5° circular target was centred 10° off-axis along the horizontal meridian, and measurements are for the right eye. The target was presented for 100 ms against a 17° diameter, circular background which had a fixed spectral component of wavelength 515 nm, and luminance 1.0 log troland, and a second component of wavelength $\mu$ and adjustable radiance. (a) Data for a 650 nm target, recorded from the left, normal hemifield (filled circles) and right 'blind' hemifield (open circles). The broken line represents the former data, displaced for comparison with the latter, and the dotted line the average normal F44 spectral response (Wyszecki & Stiles 1982). (b) Data for a 515 nm target, for the left, normal hemifield (filled circles) and for the right 'blind' hemifield (open circles). The broken line represents the former displaced for comparison with the latter, and the dotted line the average normal F44 spectral response (Wyszecki & Stiles, 1982). Data are for patient GY. Error bars represent the spread of data from three independent determinations.

For $\mu > 500$ nm, relative spectral sensitivity recorded for GY's right 'blind' hemifield is very similar to that recorded for his normal, left hemifield and to the average F44-spectral response (Wyszecki & Stiles 1982). The data also show that threshold sensitivity for GY's 'blind' hemifield is about 1.0 log unit lower than that for the normal hemifield, which is consistent with previously published data for GY (Barbur et al. 1980) and for other patients (Stoerig & Cowey 1991). Spectral response data measured under conditions designed for the isolation of the F44 mechanism are plotted in figure 1b. Again, for $\mu > 500$ nm, relative spectral sensitivity values for GY's 'blind' hemifield are similar to those recorded from his normal hemifield, and to the standard F44-spectral response. Detection sensitivity for the 'blind' hemifield is about 1.0–1.5 log units below that for the normal hemifield and, for $\mu < 500$ nm, relative sensitivity for the 'blind' hemifield is somewhat greater than that for the normal hemifield. Spectral responses measured with a white background field are plotted in figure 2. The broad-band spectral response recorded for GY's blind hemifield is very similar to that for the normal control PB, except that sensitivity values are about 1.5 log units lower. At wavelengths $\lambda \leq 500$ nm, the responses differ significantly from the photopic spectral sensitivity function standardized by the Commission Internationale de l'Eclairage (CIE).

Discrimination data are presented in figures 3 and 4. The probability of identifying a white target of luminance $L$ as brighter than a reference target of luminance 2.2 log trolands, measured for GY's 'blind' hemifield, is plotted in figure 3a, and the data demonstrate that GY readily distinguishes relative brightness with his 'blind' field. Results of the colour-naming experiments are summarized in figures 3b and 4. The probability with which GY names correctly 'red' (665 nm), 'green' (535 nm) and 'blue' (440 nm) stimuli presented within the 'blind' hemifield rises monotonically as stimulus luminance increases, reaching approximately the same value for each at a luminance of 2.1 log troland (figure 3b), and the
Figure 3. Discrimination data; the data shown in both (a) and (b) were measured for the field configuration illustrated in the inset of (b). The white hemifield \( W \), of fixed luminance 1.5 log troland, was continuously visible, as was the fixation point, \( F \). (a) Brightness discrimination data for pairs of white light stimuli, presented successively for 500 ms with a 500 ms interval, which occupied the right half of the stimulus (field shown in the inset). The probability, \( p \), of identifying a stimulus of luminance \( L \) log trolands as brighter than the reference stimulus (luminance 2.2 log trolands) is plotted against \( L \). Open circles, patient GY; filled circles, normal control ML. Data are for 20 presentations of each stimulus, luminance \( L \), \( \lambda \) colour discrimination data for the patient GY. The probability, \( p \), of naming correctly a stimulus of wavelength \( \lambda \) presented for 500 ms is plotted against the stimulus luminance, \( L \). Open circles denote the probability of naming a 665 nm stimulus ‘red’, crosses are the probability of naming a 550 nm stimulus ‘green’, and squares the probability of naming a 440 nm stimulus ‘blue’. Threshold luminance, \( L \), for detection of these three stimuli are marked by arrows along the abscissa. Values refer to 20 presentations for each data point.

Histograms of figure 4 all refer to stimuli of this luminance. GY achieves discrimination at well above chance (\( p = 0.33 \)) level in several tasks using the large (40° diameter) field, but his performance is best for long-wavelength stimuli, for which he can distinguish, at greater than chance level, near monochromatic stimuli which differ in wavelength by only 30 nm (figure 4b,c), and stimuli distinguished by saturation (figure 4e). With a smaller (10° diameter) field, however, performance deteriorates, even for coarse discrimination of monochromatic stimuli distinguished by large differences in wavelength (figure 4b). Data for the control subject, PB, and for GY’s normal hemifield, established that the colours of the monochromatic stimuli could be identified correctly at or within 0.5 log units of threshold luminance, except for those of figure 4f, which involve the discrimination of a monochromatic green from white and from a desaturated green.

4. DISCUSSION

Our results demonstrate activity of both the \( \Pi_3 \) (blue-sensitive) and \( \Pi_4 \) (green-sensitive) cone mechanisms in visual detection thresholds recorded for GY’s ‘blind’ hemifield (figure 1a,b). At wavelengths below 500 nm, the relative sensitivities of these spectral functions are raised in comparison with those measured for GY’s normal hemifield and with the average foveal data published by Wyszecki & Stiles (1982). We failed to isolate the \( \Pi_3 \) (blue-sensitive) spectral responses in measurements on GY’s ‘blind’ hemifield with a 440 nm test stimulus, obtaining instead a \( \Pi_0 \) (rod) spectral function. We attribute the raised short-wavelength sensitivities of the \( \Pi_3 \) and \( \Pi_4 \) spectra recorded for GY’s blind hemifield to rod intrusion in the detection process. The spectra recorded with a white background follow the photopic \( V \) curve at wavelengths greater than 520 nm, but exhibit increased sensitivity at shorter wavelengths, both for GY’s ‘blind’ hemifield and for the normal control (figure 2). We again attribute the latter to rod activity and, despite the indication of a shoulder in the spectral responses at around 600 nm, our data do not provide strong evidence for the colour-opponent response features observed under foveal viewing conditions (Sperling & Harwerth 1971; King-Smith & Carden 1976). Stoerig & Cowey (1989, 1991) report spectral response characteristics similar to those of figure 2 for two of three hemianopic patients, but their data provide a clearer indication of colour-opponent responses for short-wavelength stimuli. Rod intrusion in GY’s spectral responses was also apparent in spectral measurements made with the left eye. These gave a pure \( \Pi_0 \) (rod)-spectral response under conditions identical to those which, for the right eye, generated the colour opponent responses of figure 2. Asymmetries between ‘blindsight’ responses arising in the ‘nasal’ and ‘temporal’ projection pathways have been noted by Rafal et al. (1990).
different stimuli are completely unrelated to their suprathreshold luminances. With his 'blind' hemifield, GY is able to discriminate relatively small wavelength steps at the long-wavelength end of the spectrum (e.g. 615 nm from 665 nm (figure 4b) and from 585 nm (figure 4c)), and can discriminate between red, pink and white (figure 4e). He is much more secure with short-wavelength stimuli, and frequently confuses 440 nm and 525 nm, even with the coarse wavelength steps of figure 4a, and is unable to distinguish between white and short-wavelength stimuli (figure 4f, g). His discrimination performance falls almost to chance levels with a smaller, 10° diameter field (figure 4b), which is presumably why he failed to discriminate red from green in an earlier study (Blythe et al. 1987). In contrast, Stoerig (1987) established red-green discrimination in patients with targets of 46° diameter, although she used receiver operating characteristic analysis. Atrophy of retinal ganglion cells in destriate monkeys is dependent on the age at which the cortex is ablated (Dineen & Hendrickson 1981; Weller & Kaas 1989), and Stoerig & Cowey (1991) argue that the length of time for which an individual patient has suffered a striate lesion is an important factor in performance of tasks such as wavelength discrimination. GY's traumatic lesion was incurred in childhood, and retrograde degeneration of his visual pathways should be well advanced. His failure to achieve significant wavelength discrimination with his 'blind' hemifield unless presented with large stimuli may, therefore, be due to a paucity of the cone-driven neural elements required for such discriminations.

GY's MRI scans provided no evidence of surviving neural tissue in the left striate cortex outside the region surrounding the pole. Fendrich et al. (1992) reported that a patient with a dense, left hemianopia, who exhibits 'blindsight' within restricted regions of the scotoma, has localized sparing of neural tissue in the striate cortex, although it was not established whether retinal projection of the former area to the striate cortex coincides with the latter. GY can detect transient stimuli at all points in his 'blind' hemifield, along all radial directions extending to the very periphery of the field, thus localized sparing of the striate cortex cannot explain his residual vision. Our spectral response data confirm Stoerig & Cowey's (1989, 1991) finding that both rods and cones contribute to 'blindsight' responses. Cone activity is observed in the retinal projection to the monkey superior colliculus (Kadoya et al. 1971; Marrocco & Li 1977), and colour-opponent responses have been recorded from neurons in the pulvinar (Felsten et al. 1983), thus non-geniculate projections could support the psychophysical spectral response data. Destriate monkeys can perform red-green colour discriminations (Schilder et al. 1972), and monkeys lacking both striate and pre-striate cortical areas can discriminate between blues and greens (Keating 1979). GY achieves robust performance in discrimination for long-wavelength stimuli, but is less successful with short wavelengths, perhaps because of the significant rod contribution evident in his spectral responses. MRI scans show that GY's lesion invades those areas in the lingual and fusiform gyri which are

Figure 4. Colour discrimination data for the patient GY obtained with a field similar to that illustrated in the inset to figure 3, but with the fixation displaced such that vertical border between the hemifields was located 17° off-axis. Each histogram gives the probability, p, of naming correctly each of the group of three stimuli used in a particular experiment. Data are for 10 presentations of each stimulus at luminance level 2.1 log trolands; p values for colour naming refer to the following combinations of descriptions and stimuli: (a) 665 nm, 'red' (open column); 553 nm, 'green' (hatched); 440 nm, 'blue' (double hatched). (b) 665 nm, 'red' (open); 615 nm, 'orange' (hatched); 585 nm, 'yellow' (double hatched); (c) 615 nm, 'orange' (open); 585 nm, 'yellow' (hatched); 535 nm, 'green' (d) 535 nm, 'green' (open); 490 nm, 'blue' (hatched); 455 nm, 'purple' (double hatched). (e) 665 nm, 'red' (open); white, W, added in equal photometric proportions to 665 nm, 'pink' (hatched); white W, 'white' (double hatched). (f) 535 nm, 'green' (open); white W, added in equal photometric proportions to 535 nm, 'blue' (hatched); white W, 'white' (double hatched). (g) 440 nm, 'blue' (open); white, W, added in equal photometric proportions to 440 nm, 'blue' (open manual); 440 nm, 'blue' (double hatched). (h) As (a) but with the test half field reduced to 10° in diameter. All stimuli were adjusted to a luminance of 2.1 log trolands. A probability of 0.75 is statistically significant at 0.01 level.

GY exhibits near-normal brightness discrimination for his 'blind' hemifield (figure 3a), and the possible confusion between brightness and colour is clearly important in the assessment of his ability to discriminate between coloured stimuli. The data of figure 3b refer to a stimulus set incorporating variations in both wavelength and luminance. The data show improved discrimination with increased luminance for all three wavelengths, and are inconsistent with identification of stimulus colour based on differences in luminance detected by a unitary spectral response mechanism, because the names attributed to the
involved in human visual responses to colour (Lueck et al. 1989), and are considered homologous to the colour-sensitive V4 area in the macaque (Zeki 1980). GY reports that he perceives no colour sensation in response to light stimulation of his 'blind' hemifield, and that his verbal responses in wavelength discrimination experiments are based on 'feelings' rather than perception. Such subjective observations are typical of patients who attempt to explain the basis of their performance in experiments which involve 'blindsight' discriminations (Weiskrantz 1986, 1990). Both rods and at least two spectral classes of cones contribute to visual detection in GY's 'blind' hemifield, and activity of more than one spectral class of photoreceptor is a requisite for visual discriminations based on spectral composition. The lesion in GY's left occipital lobe spares the area corresponding to MT (V5), the motion-sensitive area of the pre-striate cortex, and, correspondingly, he responds well to moving or transient stimuli. The lingual, but not the fusiform, gyrus is involved in the left cortical lesion, thus the pre-striate areas which in man appear to be involved in the central processing of colour (Meadows 1974; Lueck et al. 1989; Zeki 1990) are at least partly damaged. GY's poor performance in the discrimination of colours may, therefore, reflect the damage incurred in this cortical area.

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