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Spatial and temporal response properties of residual vision in a case of hemianopia

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SUMMARY

Residual vision in subjects with damage of the primary visual cortex (striate cortex) has been demonstrated in many previous studies and is taken to reflect the properties of known subcortical and extrastriate visual pathways. In this report we describe psychophysical experiments carried out on a subject clinically blind in half of his visual field (i.e. homonymous hemianopia) caused by striate cortex damage. They reveal the existence of two distinct channels mediating such vision. One channel responds to spatial structure and the other to light flux changes. The spatially tuned channel has a peak response at about 1.2 cycles per degree and shows rapid loss of sensitivity at both high and low spatial frequencies. This channel does not respond to diffuse illumination. The light flux channel, however, responds only to sudden increments in light flux levels on the retina and shows extensive spatial summation. Both channels require transient inputs, with a peak sensitivity at about 10 cycles per second and show virtually complete attenuation at temporal frequencies below 2 cycles per second. The spatiotemporal characteristics of these two channels account for much of the reported limits of visual performance attributed to subcortical or extrastriate pathways in some patients, and especially for their relatively good sensitivity for the detection of abrupt, transient stimuli or fast-moving targets. A new method is also applied to the measurement of the amount of light scatter in the eye. The measurements show that light scatter into the sighted hemifield could not account for the results obtained with the stimuli used to characterize the residual vision of this subject.

1. INTRODUCTION

The 'primary visual cortex' (V1, or striate cortex) is not the only target in the primate brain to receive signals from the retina, although the pathway to it (the geniculostriate pathway, from retina to lateral geniculate nucleus of the thalamus to striate cortex) is the largest and the most thoroughly studied. There are nine other known pathways from the retina to other brain regions (Cowey & Stoerig 1991*a*), and even the lateral geniculate nucleus itself also sends a small projection to the prestriate cortex that is independent of its major projection to V1 and survives in the absence of V1 (Yukie & Iwai 1981; Yoshida & Benevento 1981; Fries 1981; Cowey & Stoerig 1991*b*).

Given these parallel inputs it is not surprising that, in monkeys and other mammals that have been studied, visual discriminations are still possible following removal of V1, although the capacity is altered in various ways (cf. review by Weiskrantz 1986). In man, damage to the geniculostriate projection or to the striate cortex results in what are defined clinically as blind areas in the corresponding parts of the retinal–cortical map. In spite of what can appear to be a complete loss of visual function in such patients, many psychophysical studies have revealed residual visual capacity in patients with damaged central visual pathways (Poppel *et al.* 1973; Weiskrantz *et al.* 1974; Barbur *et al.* 1980). Although a variety of reports have appeared concerning the many different aspects and features of residual capacity in subjects with scotomata caused by visual cortical damage, in none has a systematic and basic specification been made of the spatiotemporal properties of the residual visual channels. The purpose of this study was to obtain such a specification.

As residual vision in patients with damaged geniculo-striate projections does not involve normal visual experience (blindsight, cf. Weiskrantz 1986, 1990), it is necessary to exploit psychophysical methods that are not dependent on the subject's verbal descriptions of visual events. One set of methods uses two-alternative forced-choice psychophysical procedures in which stimulus alternatives are presented to the 'blind' field and the subject is instructed to 'guess' which of two alternative stimuli was presented, or whether a stimulus was presented at one or another particular time interval, regardless of whether there was actually any experience of the stimulus. There are other methods that are indirect and independent of forced-choice psychophysics (cf. Weiskrantz 1990).

The present study is directed towards specifying the spatial and temporal properties of the neural mechanisms that limit residual vision in a subject with hemianopia. G.Y., the subject of this study, has been investigated in several previous studies (Barbur *et al.*

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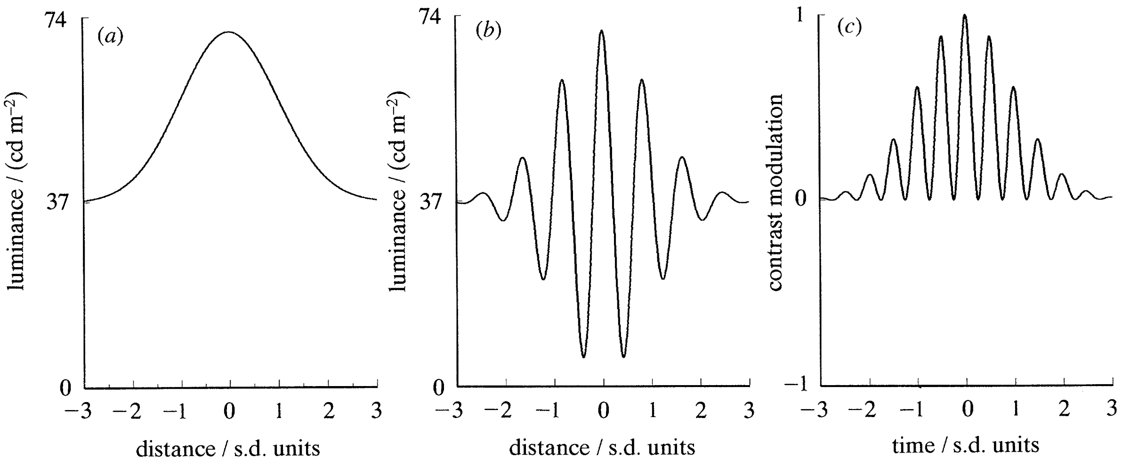

Figure 1. Schematic representation of the spatiotemporal luminance profiles of the visual stimuli used in this investigation. The visual stimuli were either (*a*) unstructured, i.e. uniform Gaussian blobs which cause a net increase in light flux level on the retina, or (*b*) Gaussian-weighted, sinusoidal gratings of space averaged luminance equal to that of the uniform background. (*c*) The luminance profile, in the case of Gaussian blobs, and the spatial contrast, in the case of sinusoidal gratings, were modulated in time using Gaussian-weighted, sinusoidal modulation. The standard deviations selected for the spatial and temporal Gaussians were 3.3 deg and 0.5 s, respectively. The spread of the visual stimuli in both space and time is terminated at ± 2 s.d.s. The uniform background had a luminance of 37 cd m^{-2} and subtended a visual angle of 25 deg × 20 deg. The stimulus was centred 12.5 deg away from the fixation target in the blind hemifield and 9 deg above the horizontal meridian. Maxwellian contrast is used throughout and the modulation depth, in the case of unstructured uniform blobs, describes the peak luminance increment with respect to the uniform background, i.e. 100% modulation corresponds to a peak luminance of a Gaussian blob equal to twice that of the uniform background.

1980, 1988; Blythe *et al.* 1987; Weiskrantz *et al.* 1991). The results of these studies demonstrated residual visual capacity for spatial localization, motion detection and speed discrimination, pupil reflex responses, and goal-directed saccadic eye movements.

G.Y. is known to have good ability in his defective visual field to discriminate the direction of a moving visual stimulus, depending on its velocity (Barbur *et al.* 1980). He also is known to perform well in psychophysical experiments when presented with abrupt, transient stimuli, a capacity that is size dependent (Weiskrantz *et al.* 1991; Stoerig & Cowey 1989). As a result of such existing knowledge on the properties of G.Y.'s residual vision, we were able to devise visual stimuli and modes of presentation which make possible the measurement and characterization of the spatiotemporal limits of his residual capacity.

In a previous study, following Hess & Pointer (1989), we used visual stimuli which allowed us to control the abruptness or gradation of the spatial edges as well as the temporal onsets and offsets in a simple and specifiable way. This was achieved by imposing smooth functions (Gaussian envelopes) in both the spatial and temporal domains. The slope of the gradients is specified by the standard deviation (see figure 1) of the Gaussian function. We found that for G.Y. there was a very strong dependence of forced-choice 'guessing' results on the standard deviation (s.d.) of the temporal Gaussian function (Weiskrantz *et al.* 1991). Given an adequate stimulus size, a temporal onset–offset s.d. of less than 200 ms was sufficient to generate high levels of detection performance in a two-alternative forced-choice psychophysical paradigm. Standard deviations of 250 ms or more produced chance performance, confirming the negative findings of Hess & Pointer (1989) with this and other subjects using similar, but slightly smaller, sized stimuli and a s.d. of 250 ms.

The results obtained from these earlier studies enabled us to select stimuli with a temporal Gaussian parameter that was clearly outside the range of effective transient envelopes per se (i.e. a large temporal s.d. for which the subject's responses are at chance level in the absence of any other form of temporal modulation). We also used visual stimuli that were clearly above the threshold for size, the spatial borders themselves being Gaussian limited. Having selected appropriate standard deviations for the spatiotemporal Gaussian functions, we could then investigate the effect of temporal modulation frequency on stimulus detection performance for both grating stimuli and uniform blobs. The effect of grating spatial frequency was also investigated at a fixed temporal modulation frequency. All experiments used a two-alternative forced-choice testing procedure.

We also investigated the light-scattering properties of G.Y.'s eye and the minimum conditions required to eliminate the detection of scattered light. The possibility had been raised (cf. Campion *et al.* 1983) that 'blindsight' might have been based on the spread of light from the blind regions into normal regions of the field. Such an explanation could be eliminated in previous studies of G.Y. (cf. Barbur *et al.* 1980) by the use of large, uniform backgrounds of high luminance against which scattered light could not be detected. The visual stimuli used in the present study were quite different from those used in earlier investigations, and it was therefore considered prudent to measure the light-

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scattering parameters of this subject's eye and the minimum background luminance required to eliminate the detection of scattered light. This measurement was based on a new method developed for the measurement of scatter in normal vision (Barbur *et al.* 1993). The results demonstrate clearly that scattered light can be ruled out as a basis of the subject's residual vision for the stimulus conditions used in the current study.

2. METHODS

(*a*) *Apparatus*

The psychophysical investigations reported here were done on the P_SCAN system which was designed for simultaneous, binocular measurements of pupil size and the corresponding movements of the eyes (Barbur 1991). The apparatus incorporates a high resolution, 20 inch, colour graphics display (Model HP D1187A) which allows the generation of a range of stimuli, with good control of contrast and chromaticity. The 60 Hz non-interlaced, graphics adapter (Model HP A1083A) supports a screen resolution of 1280 × 1024 pixels with 256 simultaneous colours selected from a palette of 16.7 million. A luminance calibration program allows automatic calibration of the luminance of each phosphor for each of the 256 voltage values which can be applied to each gun. The calibration is carried out using an LMT 1003 luminance meter, and the measured luminance values are stored in a calibration file and used by each experimental program to generate the required luminance at a corresponding location in the visual stimulus. A Vectra $R^S/25C$ computer fitted with a mathematics coprocessor and running at 25 MHz is used for the generation of the visual stimuli, the control of the P_SCAN apparatus and to record the subject's responses. For the highest temporal modulation frequency used, the colour display was replaced with a Tektronix 608 monitor driven by an analogue visual pattern generator. Square-wave temporal modulation of stimulus luminance up to a frequency of 100 Hz can be achieved using this monitor.

For the majority of experiments, the subject viewed the 20 inch display from a distance of 0.8 m and his head movements were restrained by means of an adjustable chin and head support unit. A white screen which approximates a Lambertian surface was mounted on the ceiling, vertically above the monitor, and was illuminated by a partly collimated, tungsten-halogen source, driven from a stabilized supply. This arrangement of diffuse illumination ensures a steady state of light adaptation without contributing significantly to the luminance of the display.

(*b*) *Visual stimuli for investigating spatiotemporal characteristics of residual vision*

Two classes of visual stimuli were used. These were either structured patterns consisting of sinusoidal gratings, or unstructured Gaussian blobs. The spatially structured stimulus is defined according to the following equation, where z represents distance away from the centre of the stimulus and can be expressed as $z=(x^2+y^2)^{1/2}$, with x and y representing the location of the point of interest in Cartesian coordinates.

$$L(z,t)=L_0\{1+0.5\cdot c\cdot G(z)\cdot\cos(2\pi xs)\cdot[1+\cos(2\pi tf)]\cdot G(t)\},$$

where s and f represent the spatial and temporal modulation frequencies of the stimulus, c represents the contrast or modulation depth variable, and $G(z)$ and $G(t)$ represent the spatial and temporal Gaussian weighting functions, i.e.

$$G(z)=\exp[-(z-2\cdot\sigma_z)^2/2\cdot{\sigma_z}^2] \quad \text{and} \quad G(t)=\exp[-(t-2\sigma_t)^2/2{\sigma_t}^2].$$

The spatial and temporal spread of the visual stimuli were limited to plus and minus two Gaussian standard deviations. The values selected were $\sigma_z=3.3$ deg and $\sigma_t=0.5$ s. These values ensured that the stimuli were all above threshold for size at the optimum temporal frequency, but well below threshold for eliciting a response from a temporal transient associated only with the Gaussian envelope.

The uniform Gaussian blob stimulus which causes a net increase in light flux level on the retina is defined as follows:

$$L(z,t)=L_0[1+0.5\cdot c\cdot G(z)\cdot[1+\cos(2\pi tf)]\cdot G(t)].$$

All stimuli were presented to the blind hemifield of the hemianopic subject against a uniform background field of 25 deg × 20 deg and luminance 37 cd m^{-2}. The centre of the stimulus was located 12.5 deg from fixation and 9 deg above the horizontal meridian. The uniform Gaussian blob causes a net increase in light flux level on the retina; its luminance profile is shown in figure 1*a*. The space-averaged luminance of the structured stimulus remains unchanged with a luminance profile as shown in figure 1*b*. The typical, temporal modulation profile applied to both uniform blobs and structured stimuli is shown in figure 1*c*. In the case of uniform blobs, the peak luminance change is expressed as a percentage of background luminance. For example, a modulation depth of 100% corresponds to a peak luminance in the blob stimulus twice that of the uniform background.

(*c*) *Visual stimulus and method used for the measurement of scattered light*

The distribution of scattered light, in the case of small point sources, is described well by the following empirical light scatter equation:

$$L_s=k\cdot E/\theta^n \tag{1}$$

(where k and n are constants for a given observer, θ represents the eccentricity of the point stimulus, and E represents the illuminance level in the plane of the cornea (Stiles 1929)). Our aim is to measure accurately the straylight factor, k, and the scatter index, n, which define the light scatter equation, from measurements of light scattered by an extended source. The general approach is to use a nulling technique so that

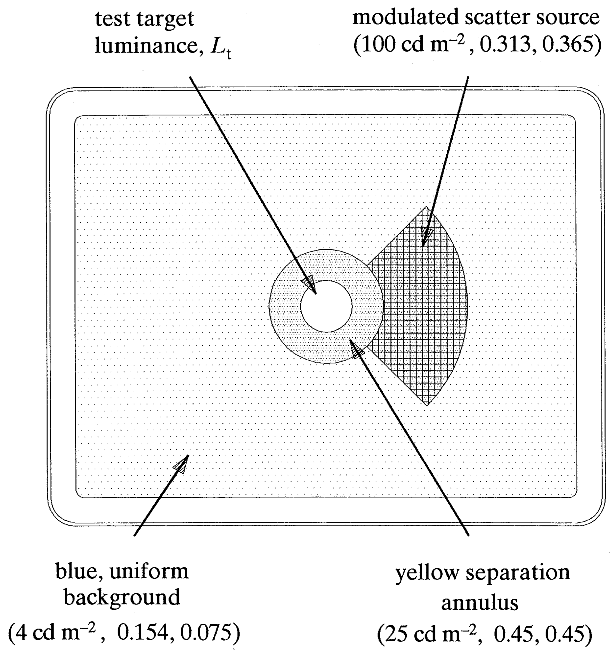

Figure 2. Diagram showing a schematic representation of the stimulus configuration designed for the measurement of light scattered by the dioptrics of the eye. The light-scatter program is implemented on the P_SCAN 100 system, which also allows simultaneous measurement of pupil size (Barbur 1991). The peak luminance of the scattering source is 100 cd m^{-2} and this is modulated sinusoidally at a frequency of 8.6 Hz. The test stimulus was usually positioned in the centre of the display and its luminance is again modulated sinusoidally at the same temporal frequency, but in counterphase with the scattering source. The effective eccentricity of each annulus is computed by integrating the light scatter equation over the extended source. The best-fit light scatter model parameters are then obtained by using error-weighted, iterative regression analysis from the measured experimental data and the computed effective eccentricities of the scattering annuli.

acceptable limits for using the high luminance peripheral annulus can be measured.

Figure 2 shows a schematic representation of the stimulus configuration used in the measurement of scattered light. The dark shaded sector annulus is an extended scattering source and has a peak luminance of 100 cd m^{-2}. The method makes use of a flicker compensation technique (van den Berg 1986; van den Berg & Spekreijse 1987), modified for use on a visual display (Barbur *et al.* 1993). The technique counterphases the modulation of the annulus and that of the stimulus so as to determine the null condition. For normal measurements of scattered light, the scattering source is a full annulus of large width which varies in eccentricity and size. For each annulus width, the annulus area was adjusted so as to ensure that the total flux entering the eye was constant (Barbur *et al.* 1993). The luminance of the annulus is modulated sinusoidally at maximum amplitude, at a frequency of 8.6 Hz. The test stimulus is also modulated sinusoidally at the same frequency, but in counterphase with the scattering source. For each scatter source annulus, the mean luminance of the test stimulus is increased systematically until its retinal illuminance equals that caused by scattered light which nulls the perceived flicker.

The parameters which describe the amount and the angular distribution of scattered light in the eye can now be extracted from the measured data by using iterative computational procedures. The effective eccentricity, θ_c, of each annulus, defined as the eccentricity of a very narrow ring which would generate the same amount of scattered light as the broad annulus for the same illuminance level in the pupil plane, is calculated for a given value of n by integrating the scatter function (equation (1)) over the annulus. For each set of effective eccentricities computed in this way, error-weighted, linear-regression analysis on the measured scattered light levels yields a value of n and k. The procedure is repeated until the regression analysis on the measured data yields the same value of n as that used for the computation of effective eccentricities.

In addition to a full-size scattering source, the experiments with the hemianope also used 90 deg sector annulus, which spanned a range of eccentricities along the horizontal meridian, both in the sighted and the blind hemifields (see figure 2). The light scattered from the sector annulus is reduced significantly by comparison with the full annulus, and the results are shown in figure 7*a,b* for a normal subject and for G.Y.'s blind and sighted hemifields.

In a separate experiment, we no longer measured the level of scattered light generated by the flickering sector annulus, but the minimum steady luminance of the test field which makes the scattered light caused by the sector annulus undetectable. The test stimulus was no longer modulated sinusoidally, but its luminance was increased systematically for each scatter source eccentricity until the detection of flicker was completely eliminated. This experiment provides a direct measure of the minimum background field luminance which is required to eliminate the detection of scattered light even under stimulus conditions which generate large scatter levels.

3. PROCEDURE

(*a*) *Spatiotemporal properties*

The subject's ability to respond to a visual stimulus was measured by using a two-alternative, forced-choice procedure. The stimulus was presented in one of two intervals, each of 6 s duration. The two intervals were signalled to the subject by means of auditory beeps. The interval which the stimulus was assigned was random. The parameter under investigation, such as the spatial and temporal frequency, was also assigned randomly in every trial. The subject was required to indicate verbally whether a stimulus was presented after the first or the second. The subject was forced to respond in this way whether or not he actually 'saw' the stimulus. Appropriate response buttons were pressed by the experimenter to record the subject's response and to trigger the next trial. Fixation stability was monitored throughout, and fixation drifts for this subject were found to be less than 40 min arc (Barbur *et al.* 1988; Weiskrantz *et al.* 1991). During a single experimental session either the spatial or the temporal frequency of the stimulus was varied systematically. When investigating the spatial frequency response, the contrast of the grating was modulated at a temporal frequency of 6 Hz. The temporal frequency response of the spatially tuned channel was measured with a grating of spatial frequency 1.1 c deg^{-1}. Sinusoidal temporal modulation of grating contrast was achieved up to a frequency of 12 Hz. Frequencies of 15 Hz, 30 Hz and 50 Hz were tested with square-wave temporal modulation. The higher harmonics in the square-wave condition are of small amplitude by comparison with the fundamental frequency, and are all above 45 Hz, when the eye's sensitivity to flicker is reduced significantly (de Lange 1954). On average, each stimulus parameter was presented 36 times, and the results are presented as correct percentage response scores.

(*b*) *Scattered light*

A modified staircase procedure was used to estimate the mean retinal illuminance of the test stimulus caused by scattered light. The luminance of the scattering source (see figure 2) was modulated intermittently to cause bursts of flicker lasting for 1 s. Following each presentation, the subject had to indicate the presence or absence of perceived flicker by pressing an appropriate response button which also initiated the next presentation. The mean, modulated luminance of the test stimulus, for the first presentation in the sequence, was always 0 cd m^{-2}. As the test stimulus luminance was increased systematically in sequential presentations of the same scatter source, perceived flicker was first eliminated and then seen again when the retinal illuminance caused by scattered light was overcompensated by modulation of the stimulus amplitude. The sequence was then reversed with smaller step changes in test stimulus luminance until the condition of zero flicker was again established. Six such estimates were obtained and averaged for each scatter source eccentricity.

4. SUBJECT

The subject of this investigation was involved in a car accident when 8 years of age. Head damage resulted in intracranial haemorrhage. Unilateral, localized degeneration in his left occipital lobe followed this injury and is likely to have been caused by ischemia of brain tissue. As a result of the accident, subject G.Y. is clinically blind in his right hemified, with approximately 3 deg of macular sparing (Barbur *et al.* 1980). This homonymous hemianopia is consistent with results of computed tomography (CT) scans (Blythe *et al.* 1987) and more recent magnetic resonance imaging (MRI) scans (K. H. Ruddock, personal communication) which show complete unilateral damage to the left striate cortex except for tissue corresponding to macular sparing. The subject's visual field sensitivity has remained more or less constant since the time of the accident. Colour discrimination, visual acuity,

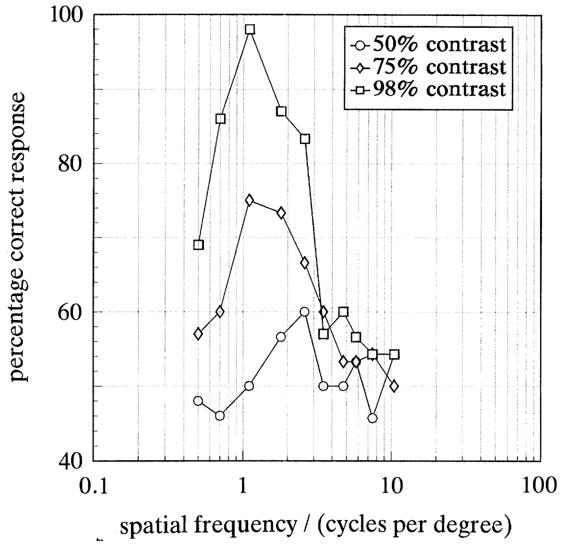

Figure 3. Percentage correct discrimination scores plotted against the spatial frequency of the sinusoidal grating. Randomly interleaved stimulus presentation was used throughout, and each stimulus frequency was presented 36 times. The spatial and temporal standard deviations of the Gaussian weighting functions were 3.3 deg and 0.5 s, respectively. The contrast of the spatial grating was modulated sinusoidally throughout at a temporal frequency of 6 Hz. The data plot results obtained for a grating contrast of 0.98 (squares), 0.75 (diamonds) and 0.5 (circles). Subject was G.Y. (blind hemifield).

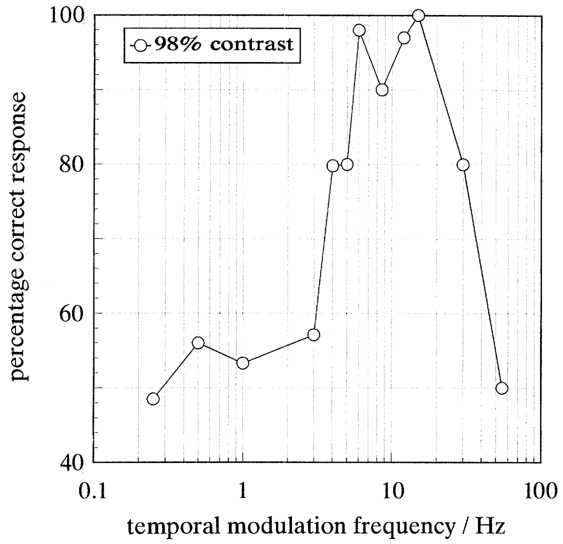

Figure 4. Results showing the temporal response characteristics of the spatially tuned channel. The spatial frequency of the grating was fixed at 1.1 c deg^{-1} (i.e. the peak sensitivity of the spatially tuned channel, as shown in figure 3). The spatial and temporal standard deviations of the Gaussian weighting functions were again fixed at 3.3 deg and 0.5 s, respectively. The grating contrast was 0.98 and, on average, each temporal frequency was presented to the subject 36 times in a randomly interleaved sequence. Subject was G.Y. (blind hemifield).

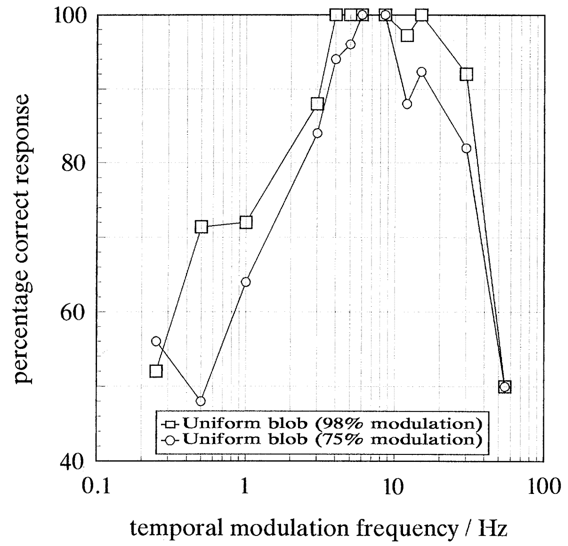

Figure 5. Results showing the temporal response characteristics of the light flux discriminating channel measured by using sinusoidal luminance modulation of the uniform, Gaussian-weighted blobs. Percentage correct discrimination scores are plotted as a function of temporal modulation frequency for modulation amplitudes of 0.98 (squares) and 0.75 (circles). Subject was G.Y. (blind hemifield).

contrast sensitivity and motion perception were found to be normal when tested foveally or in his sighted hemifield. At the start of this study, which extended over 2 years, G.Y. was aged 34.

5. RESULTS

(*a*) *Responses to spatially structured stimuli*

(i) *The spatial frequency tuning of G.Y.'s blind hemifield responses*

Results of earlier investigations with G.Y. (Weiskrantz *et al.* 1991) showed that a chance level of performance was obtained even with stimuli of large size, when the standard deviation of temporal Gaussian weighting function exceeded about 250 ms. In this experiment, the spatial and temporal standard deviations of 3.3 deg and 500 ms were used throughout. The contrast of the grating was modulated sinusoidally at a fixed temporal frequency of 6 Hz. The results obtained by using the two-alternative forced-choice procedure are plotted as a function of grating spatial frequency in figure 3 and show a peak response sensitivity for a grating spatial frequency of about 1.2 c deg^{-1} with virtually no significant response above 8 c deg^{-1}. The surprising finding is that sensitivity to gratings, as measured in terms of percentage correct discrimination scores, also falls off rapidly in the very low frequency range (i.e. 0.2–0.8 c deg^{-1}). Lower spatial frequencies were not investigated because the limited size of the Gaussian weighting function makes it difficult to maintain a constant space-averaged luminence at very low frequencies. The results do suggest, however, that in the absence of a net increment in retinal iluminance, the subject is unable to respond above chance level to grating frequencies below about 0.3 c deg^{-1}.

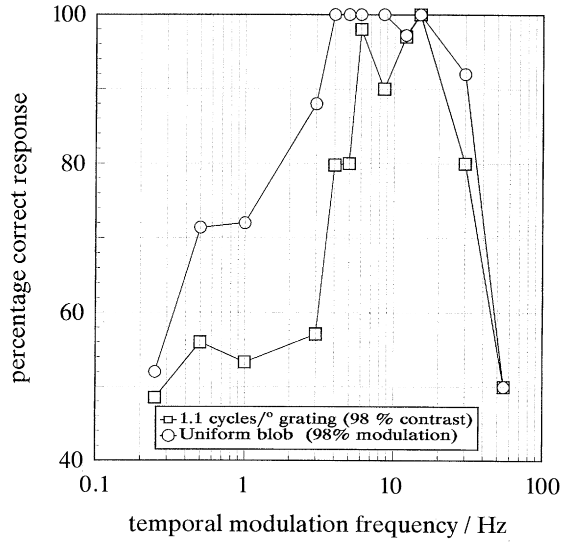

Figure 6. Comparison of the temporal response characteristics measured for the spatially tuned channel (squares) and for the light flux discrimination channel (circles) at a maximum contrast of 0.98. Subject was G.Y. (blind hemifield).

(ii) *The temporal frequency response of the spatially tuned channel*

Having established the spatial frequency response properties of the spatially tuned channel, we investigated its temporal response characteristics. A grating of spatial frequency 1.1 c deg^{-1} was selected and its contrast was modulated at a set of discrete temporal frequencies. The results plotted as percentage correct discrimination scores are shown in figure 4. The data reveal a bandpass frequency response with peak sensitivity in the high temporal frequency range and complete attenuation for temporal modulation frequencies below about 3 c s^{-1}. Because in this stimulus condition there is no change in space-averaged retinal illuminance, the data obtained are therefore likely to reflect the temporal response characteristics of the spatially tuned channel.

(*b*) *Responses to uniform blobs*

(i) *The temporal frequency response of the light flux discrimination channel*

Using the same size stimulus as in experiments with grating stimuli, the temporal response properties of the light flux discriminating channel were also investigated. The luminance of the unstructured Gaussian 'blob' was modulated sinusoidally above the level of the background field (see figure 1*c*), which generates a net increase in retinal illuminance. The results reveal a bandpass frequency response with peak sensitivity at about 10 c s^{-1}. Given the same contrast modulation, the temporal response characteristics of the light flux discrimination channel are very similar to those of the spatially tuned channel (see figure 6), although the former showed increased sensitivity with 100% correct responses observed when the contrast modulation depth was reduced to 75% (figure 5).

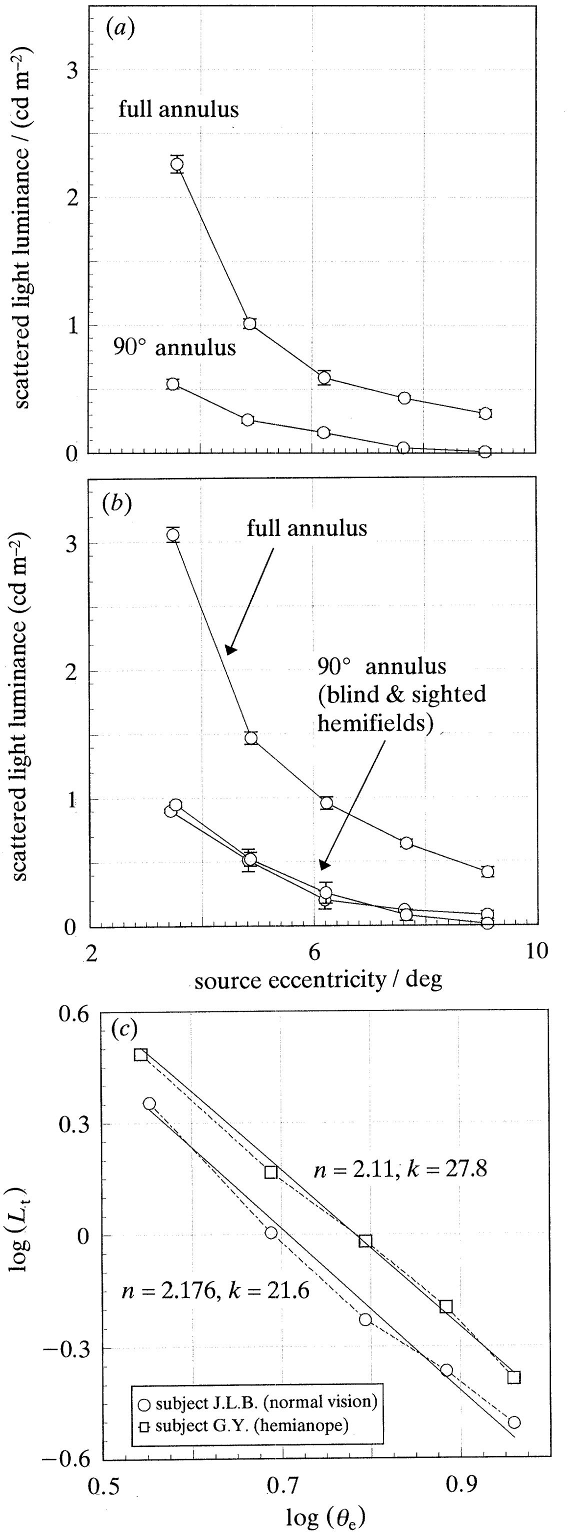

Figure 7. Measurements of light scattered over the test stimulus by a full, 360 deg annulus and by the 90 deg segment shown in figure 5, plotted as a function of scatter source eccentricity. Data are shown for (*a*) a normal subject and (*b*) the hemianope with the sector annulus presented separately both in the blind and the sighted hemifields. (*c*) The best-fit, light-scatter model parameters were computed from the experimental data (i.e. n and k in the empirical light scatter equation, $L_s = k \cdot E/\theta^n$); k and n are constants, θ represents the effective eccentricity of the annulus, and E represents the illuminance level in the plane of the cornea. The light scatter parameters of the hemianope's eye (i.e. $n = 2.11$ and $k = 27.7$) are well within the range of values which are considered to be normal (Vos 1963).

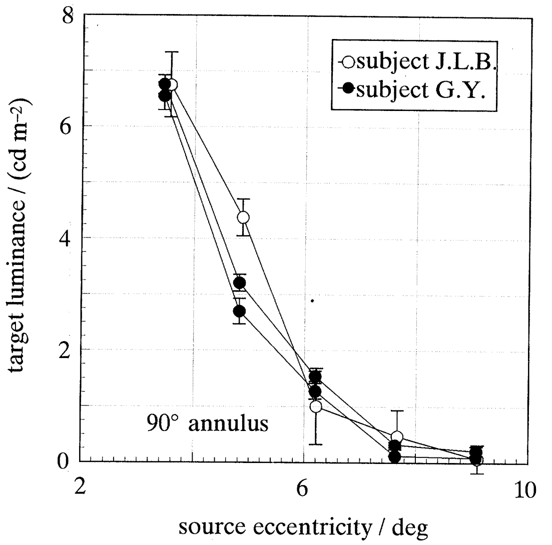

Figure 8. Measurement of background luminance level required to eliminate completely the detection of light scattered in the eye as a function of scatter source eccentricity. The results plot data for the normal subject and for the hemianope's blind hemifield. The results show that even for the stimulus parameters selected to produce large amounts of scattered light (i.e. large stimulus area and retinal illuminance change), no scattered light can be detected for a scatter source eccentricity greater than some 3.5 deg, provided the luminance of the uniform background field is greater than 7 cd m^{-2}. The error bars plot 2 standard errors obtained from six estimates of background luminance.

(*c*) *The measurement of scattered light*

The luminance of the test stimulus which produces the same retinal illuminance as that caused by scattered light is plotted in figure 7 as a function of scatter source eccentricity for both the full annulus and for the 90 deg sector source. Data are shown for a normal subject (figure 7*a*) and for subject G.Y. with the sector stimulus imaged separately in the sighted and the blind hemifields (figure 7*b*). The results of the analysis of the scattered light data together with the best-fit, light-scatter model parameters for the two subjects are shown in figure 7*c*. The minimal steady field luminance which is sufficient to eliminate the detection of flicker caused by scattered light was measured as a function of scatter source eccentricity for the 90 deg sector target (figure 8). The results of figure 8 show that, even for an effective source eccentricity of 3.5 deg, a uniform background luminance of 7 cd m^{-2} is sufficient to eliminate the detection of flicker caused by scattered light.

6. DISCUSSION

(*a*) *The measurement of scattered light*

Although the onset of the spatially structured stimulus does not cause a net increase in light flux level on the retina, this is not the case with the uniform Gaussian blob, and therefore it is of interest to establish the minimum background luminance level which eliminates the detection of the sudden increase in scattered light caused by the presentation of the test stimulus. The results of figures 7 and 8 show that a significant amount of scattered light is present in the eye, and that for both subjects the retinal illuminance caused by scattered light at a given point on the retina decreases approximately with the square of the visual angle away from the scattering source. The best-fit, light-scatter model parameters are well within the range of values associated with normal subjects (Vos 1963). In addition to the eccentricity of an extended source, the amount of scattered light at a given point on the retina, distant from the source, is also determined by its size and luminance. The scattering source sector, which was used to measure scattered light, is of higher luminance and has a larger effective area in comparison with the Gaussian blob stimulus used in our experiments. The light scattered by the sector annulus is therefore significantly greater than that caused by the Gaussian blob. Measured with respect to the foveal region, the centre of the Gaussian blob has an eccentricity of about 9 deg of visual angle. For this scatter source eccentricity the results of figure 8 predict that, even for the high-luminance, sector annulus target, a uniform background of luminance less than 1 cd m^{-2} would be sufficient to eliminate completely the detection of scattered light. The luminance of the large uniform background field used in this investigation was 37 cd m^{-2}. Outside the 25 deg × 20 deg uniform background, in the sighted hemifield, the amount of scattered light is negligible because of the much larger eccentricities involved, and at such eccentricities there is a total absence of perceived flicker. The luminance of the remaining visual field in the extreme periphery is never less than 1 cd m^{-2} because of the ambient illumination level produced by the extended ceiling source which is used to maintain a steady state of light adaptation, and the scattered light from the steady, uniform background field.

These observations show clearly that, for the stimulus conditions of these experiments, the subject could not base his responses on the detection of light scattered into the sighted hemifield from the blob test stimulus presented 12 deg in the blind hemifield. As the safety margin as revealed by these tests is very large, one might argue that measuring the amount of scattered light and carrying out the analysis described here is unnecessary. These findings were, however, not immediately obvious, and also they cannot be generalized to all subjects and stimulus conditions. It is possible that, under less favourable conditions of stimulus presentation, subjects whose eyes have increased levels of scattered light may be able to detect scatter even at large eccentricities from the scattering source. Tests of scattered light similar to those reported here should therefore be carried out when the interpretation of results depends crucially on the detection of scattered light.

(*b*) *The spatiotemporal properties of residual vision*

The results of this investigation reveal the existence of at least two distinct functional channels, which may set limits on the properties of residual vision associated with subcortical or extrastriate pathways. The stimuli used to characterize these channels are contained in figure 1. The grating stimulus does not induce a mean change in light flux level on the retina and reveals a bandpass, spatially tuned channel with peak sensitivity in the low spatial frequency range. This channel does not respond to diffuse illumination. The Gaussian blob, however, indicates that there is a spatially diffuse, light flux discrimination channel. The effect of 'blob' size has been examined in a previous study (Weiskrantz *et al.* 1991), suggesting that the neural mechanisms involved in the detection of luminance increments in this subject's blind hemifield exhibit extensive spatial and luminance summation; these characteristics are ideal for detection of overall light flux changes and for controlling the pupil light reflex response. The characteristics of this channel are consistent with the receptive field properties of cells in the olivary pretectal nucleus, the accessory optic nucleus and the deeper layers of the superior colliculus which are known to have large receptive field sizes (Schiller & Stryker 1972; Marrocco & Li 1977).

The spatially tuned channel has a peak sensitivity at about 1.2 c deg^{-1} (figure 3) with significant loss of sensitivity at lower spatial frequencies. Spatial frequencies below 0.5 c deg^{-1} were not investigated as it is not possible to keep the size of the Gaussian weighting function constant and the space-averaged luminance of the grating equal to that of the uniform background at very low spatial frequencies. The progressive loss of sensitivity observed when grating frequency decreases from 1.1 to 0.5 c deg^{-1} suggests that this channel has no significant sensitivity to diffuse illumination. It is therefore a spatially tuned, bandpass channel which does not respond significantly to overall, diffuse changes in light flux level on the retina. The relatively good sensitivity of the extrastriate pathways in response to a large uniform Gaussian blob, as demonstrated by the results of figure 5, must therefore involve a separate channel with extensive spatial summation.

Both neural channels have high-frequency bandpass temporal response characteristics with peak sensitivity at about 10 c deg^{-1}. The measurement of the temporal response characteristics of the two channels was only made possible by using Gaussian temporal envelopes which ensured that the subject's responses could not be based on onset–offset transients, as demonstrated in a previous study (Weiskrantz *et al.* 1991). Under these conditions, sinusoidal temporal modulation was a necessary condition for the subject to exhibit any residual vision in both channels. As far as G.Y. is concerned, no residual vision has been demonstrated in the absence of temporal transients generated either by onset–offset characteristics or by temporal modulation.

The existence of these channels and their spatiotemporal characteristics are more difficult to reveal in normal vision, which is dominated by the spatiotemporal characteristics of the geniculostriate projection. Background perturbation techniques, which involve measurement of threshold retinal illuminance level for detection of a moving stimulus when presented against a grating background with alternate bars flickering at 100% modulation, reveal a spatially tuned channel in normal vision (Holliday & Ruddock 1983). This channel, referred to by the authors as the ST2 filter, has similar characteristics to that measured in G.Y. What is of interest is that the ST2 filter has a bandpass spatial response with maximum sensitivity at about 1 c $\deg^{-1}$ and remains approximately constant with eccentricity. The temporal response characteristics of this filter were found by the authors to be bandpass and to peak at about 8 Hz, although its peak sensitivity was found to shift to higher temporal frequencies with increased background luminance. The similarity between the results reported by Holliday & Ruddock (1983) and our findings suggest that the extrastriate pathway shares the same ST2 filter mechanisms that are involved in motion detection in normal vision.

The second extrastriate channel demonstrated with large Gaussian blobs in this study possesses extensive spatial summation, which may also reflect a property associated exclusively with subcortical pathways. The properties of this channel are ideal for discriminating overall light flux changes and for the control of the pupil light reflex response, which is preserved in G.Y. and other hemianopic subjects with large stimuli. The coarse tuning of the spatial channel and the bandpass temporal response characteristics of both channels with peak sensitivity in the high temporal frequency range are consistent with the properties of G.Y.'s residual vision, in particular his coarse spatial localization of briefly presented stimuli by saccadic eye movements (Blythe *et al.* 1987; Barbur *et al.* 1988) and his ability to detect flashes of light and to discriminate correctly the direction of moving stimuli in the high speed range (Barbur *et al.* 1980).

Previous results on measurements of critical flicker frequency, 30 deg in the periphery of the visual field with G.Y., showed a marked decrease in critical flicker frequency for a high retinal illuminance of the stimulus, compared with normal vision (i.e. just over 7 Hz for a retinal illuminance of 4.3 log trolands) (Barbur *et al.* 1980), which corresponds approximately to a screen luminance of ≈ 4500 cd m^{-2} (de Groot & Gebhard 1952). Other measurements of increment spectral responsivity functions in G.Y., 30 deg in the periphery, under similar stimulus conditions, also revealed a predominantly rod input (Barbur *et al.* 1980). The low critical fusion frequency observed at high retinal illuminance may reflect the poor temporal properties of saturated rod responses (Penn & Hagins 1972; Nunn & Baylor 1982). The results of more recent increment spectral sensitivity measurements with G.Y. with stimuli located 8–12 deg from fixation in the blind hemifield provide clear evidence of mixed cone input (K. H. Ruddock, personal communication; P. Stoerig, personal communication). It is therefore possible that the temporal response properties of these two channels mediating residual vision via the subcortical or extrastriate pathways may change when the background adaptation level is high and saturated rod responses are involved.

There are several anatomical possibilities that could allow the two channels of residual function to be expressed. The sensitivity to transient stimuli and, especially, G.Y.'s ability to discriminate direction of movement strongly suggest a mediation via areas that include V3 and V5 from the known electrophysiological properties of these areas (Zeki 1974, 1978; Rodman *et al.* 1987). Single neurons in V5 (also known as MT) in the primate respond selectively to the direction of motion of visual stimuli (Zeki 1974). It is also known that in primates the qualitative properties of up to half of the neurons in V5 survive total destruction of area V1 (Rodman *et al.* 1985, 1989). Hemispherectomized patients, in whom all cortical areas are removed unilaterally, can discriminate the presence or absence of movement in their blind hemifields, for which midbrain structures are presumably sufficient, but not its directionality (Perenin 1991; Ptito *et al.* 1991). The spatial frequency characteristics demonstrated in this patient might be associated with the properties of neurons in V3.

There are several routes by which information can reach V3, V5 and other cortical areas in the absence of striate cortex. There is a projection from the superior colliculus via the pulvinar to V5, and there is also a direct retinal input to the pulvinar (Cowey & Stoerig 1991*b*). Moreover, the sparsely preserved neurons in the lateral geniculate nucleus after V1 removal also have a projection to extrastriate cortical targets (Cowey & Stoerig 1991*a*). Before the two channels subserving residual visual, demonstrated in this study, can be linked with any specific or different extrastriate pathways, new data from other related investigations would have to be obtained. These investigations may involve animal lesion studies, imaging studies using position emission tomography (PET) or functional MRI scans, or systematic characterization of residual vision in hemispherectomized patients (i.e. patients with only subcortical pathways intact) and comparison with G.Y.'s results.

Although a good characterization can be made of G.Y.'s known residual visual capacity in terms of the two channels, two qualifications must be made. The first is that this characterization need not apply to all 'blindsight' subjects. Each subject's residual visual capacity will undoubtedly depend on the fine-grained and inconsistently imposed details of their lesions and their aetiology, the age at which it occurred, and probably also on formal methods of retraining afterwards. Blindsight subject D.B., whose capacities were studied extensively some years ago, showed a qualitatively rather different profile from G.Y., although there were points of overlap (Weiskrantz *et al.* 1974, 1986).

The second qualification is that these two channels do not necessarily mediate all the possible forms of residual vision that can be demonstrated in this subject. Clearly G.Y. does not see colour or show normal chromatic discrimination in the blind hemifield; however, there is unpublished evidence (P. Stoerig and K. W. Ruddock, personal communication) that his spectral responsivity function in the near periphery shows clear involvement of cone receptors, as reported for other subjects by Stoerig & Cowey (1989). Under certain stimulus conditions, G.Y. can also discriminate between visual stimuli of different wavelength from different regions of the visual spectrum when presented with randomized luminance, even though he does not 'see' colour.

Whatever additional forms of residual vision may be present in what are defined clinically as blind areas of the visual field in cortically blinded subjects, perhaps it is fair to venture that the stage of blindsight research has now gone beyond a mere compendium of various demonstrations to characterizations and models in terms of channels that can be understood, potentially, in terms of the functional properties of different visual brain structures in relation to the configuration of the actual lesions.

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