INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
I.C.T.P., P.O. BOX 586, 34100 TRIESTE, ITALY, CABLE: CENTRATOM TRIESTE

SMR.853 - 70

ANTONIO BORSELLINO COLLEGE ON NEUROPHYSICS

(15 May - 9 June 1995)

"Spatial structure of chromatically opponent receptive fields in the human visual system"

Concetta Morrone
Istituto di Neurofisiologia
Consiglio Nazionale delle Ricerche
56100 Pisa
Italy

These are preliminary lecture notes, intended only for distribution to participants.

Visual Neuroscience (1995), **12**, 103–116. Printed in the USA.

Spatial structure of chromatically opponent receptive fields in the human visual system

PASCAL GIRARD AND MARIA CONCETTA MORRONE
Istituto di Neurofisiologia del CNR and Scuola Normale Superiore, Pisa, Italy

(RECEIVED April 4, 1994; ACCEPTED July 25, 1994)

Abstract

This study investigates the receptive-field structure of mechanisms operating in human color vision, by recording visual evoked potentials (VEPs) to multiharmonic gratings modulated either in luminance or color (red-green). Varying the Fourier phase of the harmonics from 0 deg to 90 deg produced a family of stimulus profiles that varied from lines to edges. The stimuli were contrast reversed to elicit steady-state VEPS, and also randomly jittered (at a higher temporal frequency than the contrast reversal) to ensure that the evoked response resulted from the polarity reversal, rather than from local variation of luminance or color. Reliable VEPs were recorded from both luminance and chromatic stimuli at all phases, suggesting that the mechanisms sensitive to chromatic contrast and those sensitive to luminance contrast have both symmetric and asymmetric receptive fields. Contrast thresholds estimated by extrapolation of the contrast response curves were very similar to psychophysical thresholds for phase discrimination, suggesting that the VEP response is generated by mechanisms mediating phase discrimination. The results support the idea that human color mechanisms have receptive fields with a variety of spatial symmetries (including odd- and even-symmetric fields) and that these mechanisms may contribute to phase discrimination of chromatic stimuli in a similar way to what has been suggested for luminance vision.

Keywords: Visual evoked potentials, Receptive fields, Color vision, Spatial phase, Feature detectors

Introduction

Most theories of early visual analysis assume edges and lines to be rich sources of information. Given the biological importance of these features, it is plausible that a specialized neuronal machinery has evolved to detect and analyze them. Lines and edges can be detected with maximal efficiency by operators whose symmetry is matched to that of the features (Canny, 1986): for edge detection the operators should be odd-symmetric and for line detection should be even-symmetric. Expressing the same concept in Fourier terms, the phase spectra of the impulse response function of the line detector should be 0 deg or 180 deg, and that of the edge detector ±90 deg.

In their original studies of cat and monkey cortex, Hubel and Wiesel (1962,1968) described both odd-symmetric (diphasic) and even-symmetric (triphasic) receptive fields. More recent studies also report two major classes of receptive fields with even- and odd-symmetry (Pollen & Ronner, 1981, Kulikowski & Bishop, 1981) although other studies suggest that there also exist receptive fields of intermediate phases or symmetries (Field & Tolhurst, 1986; Jones & Palmer, 1987; Hamilton et al., 1989). However, all researchers agree that there exist at least two types of receptive fields with different phases.

Psychophysical studies reinforce this evidence. A variety of techniques, including adaptation, masking, subthreshold summation (Kulikowski & King-Smith, 1973), and phase discrimination (Field & Nachmias, 1984) have demonstrated the existence of at least two classes of receptive fields. The clearest evidence is the facilitation study of Burr et al. (1989), pointing to the existence of only two classes of operators, with even- and odd-symmetry, for foveal vision and suggesting that these detectors are functionally independent at threshold.

All of the studies mentioned so far have been concerned with lines and edges defined by changes in luminance. However, luminance contrast is not the only source of spatial information in a visual image. Another rich source of information is provided by color. Both psychophysical and electrophysiological evidence suggests that color is processed by specialized detectors with chromatically opponent receptive fields. Most electrophysiological studies assume them to be circularly symmetric and hence even-symmetric (Livingstone & Hubel, 1984), although other reports suggest that odd-symmetrical receptive fields may also exist in monkey visual cortex (Michael, 1978*a–c*; Thorell et al., 1984).

Recently, an electrophysiological technique has been developed to demonstrate the existence and to study edge-specific mechanisms in humans (Burr et al., 1992). The technique was

---

Reprint requests to: Maria Concetta Morrone, Istituto di Neurofisiologia CNR, V.S. Zeno 51, Pisa, Italy.

Present address of Pascal Girard: Cerveau et Vision, INSERM, Lyon (France).

to record visual evoked potentials (VEPs) in response to counterphased sawtooth gratings that were "jittered" randomly from frame-to-frame. The random jitter ensures that the response is not generated by changes in local luminance, but must reflect the activity of detectors with asymmetric receptive fields. Here we apply a similar technique to chromatic stimuli to investigate whether there exist chromatically opponent mechanisms with receptive fields of various spatial symmetries.

Methods

Stimuli

The stimuli for our experiments were red-green multiharmonic one-dimensional horizontal gratings. The patterns were generated by a 12-bit waveform generator (Cambridge Research VSG, UK), and displayed on the face of a color monitor (Barco CDCT 6551), by modulating only the red and green guns. The peak spectral response for the red phosphor was at 628 nm (CIE coordinates: $x = 0.618$, $y = 0.35$) and that of the green phosphor 531 nm (CIE coordinates $x = 0.28$, $y = 0.605$). To minimize stimulation of short-wavelength cones, the stimuli were viewed through a Kodak Wratten filter (L16) which heavily attenuates wavelengths below 520 nm. Viewed through the filter, the CIE coordinates for the red were $x = 0.651$, $y = 0.348$ and for the green $x = 0.403$, $y = 0.59$, with average luminance of 17 cd/m^2. The visible screen was 40 cm wide and 20 cm high, subtending 20 × 10 deg when viewed from 115 cm, except for two experimental sessions where the visible screen was progressively reduced with circular masks of variable diameters.

The Fourier expansion of the stimuli is given by the sum of all even and odd harmonics, with amplitude inversely proportional to frequency. The stimulus can be expressed as the sum of red and green luminance profiles [$R(x,y,t)$ and $G(x,y,t)$] given by

$$\begin{aligned} R(x,y,t) &= rL_0\left\{1 + 0.5(m/\pi) \times \sum_k [\cos(2\pi f_s kx + \phi)/kG(k)]\right\} \\ G(x,y,t) &= (1-r)L_0\left\{1 - S\,0.5(m/\pi) \times \sum_k [\cos(2\pi f_s kx + \phi)/kG(k)]\right\} \end{aligned} \tag{1}$$

L_0 is the total mean luminance (17 cd/m^2), r the color ratio (ratio of red-to-total luminance: $R/(R+G)$, m amplitude of modulation, f_s spatial frequency of the fundamental harmonic and ϕ the Fourier phase. $S = \pm 1$: when positive the red and green patterns are out-of-phase, and when negative they are in-phase. The luminance modulation could either be red-black ($r = 1$), green-black ($r = 0$), or yellow-black ($r = 0.5$ $S = -1$). The function $G(k)$ given by

$$G(k) = \exp(-k^2/(2\sigma^2)) \tag{2}$$

was used to blur the waveforms (to minimize chromatic aberration). Except where stated otherwise, the space constant σ = 10 cycles/period. The parameter ϕ determined the appearance of the stimuli, illustrated in Fig. 1. When $\phi = 0$ deg or 180 deg, the stimulus appeared as a series of thin lines of the same polarity or color (Fig. 1, top profile), and when equal to ±90 deg as a sawtooth waveform (Fig. 1, third profile from top). For intermediate values the stimuli appeared as a combination of edge and line patterns (Fig. 1, second and fourth profiles). Note again that all these waveforms have the same amplitude spectra shown in Fig. 1B for a value of σ = 10 cycles/period.

The contrast for all stimuli was defined as the square-root of the stimulus variance divided by the mean. This definition of contrast depends only on the power spectrum of the stimulus, not on the phase (see for example Burr et al., 1989), allowing for a direct comparison between stimuli of all phases. Note that with the particular Gaussian filter used in this study [eqn. (2)], the peak-to-mean amplitude of the waveform (determining Michaelson contrast) varied by more than a factor of two between sawtooths and lines.

The responses of the long- and medium-wavelength cones to the stimuli used in this study [eqn. (1)] are readily calculated from the CIE values of the oscilloscope phosphor and human cone fundamentals (Smith & Pokorny, 1975). These calculations show that L cones do not modulate at color-ratio $r = 0.43$, M cones do not modulate at $r = 0.68$, and S cones do not module at $r = 0.83$ (points of silent substitution). For $r = 0.5$, the response amplitude of L and M cones is equal and opposite and the M and L cone contrasts are attenuated by a factor of 2.7 and 7.7, respectively.

To elicit VEPs, the gratings were reversed abruptly in contrast (phase-shifted by 180 deg) periodically at a fixed temporal frequency, causing the bar or sawtooth waveforms to alternate periodically in polarity. There were two conditions of contrast reversal, illustrated schematically in Figs. 1C and 1D for the sawtooth stimulus. The temporal sequence in Fig. 1C illustrates the condition that we refer to as "steady," where the stimulus remained fixed in position for each frame, and reversed in contrast every n frames (three in this example). In this condition, the local luminance at each spatial position modulated periodically, similarly to the standard stimulus used for steady-state VEP studies to pattern stimuli (except that the luminance or chromaticity distribution is sawtooth instead of sinusoidal or checkerboard). The panel in Fig. 1D illustrates the "jittered" condition, designed to eliminate the synchronized fluctuations of local luminance or chromaticity. In addition to the periodic counterphase, the stimulus was moved to a new random position (chosen from a uniform random distribution) at a rate of at least four times that of fundamental temporal frequency (twice that of the contrast-reversal frequency). The random "jitter" causes random luminance fluctuations at every spatial position and, as contrast reversal does not affect the randomness of the luminance distributions at each spatial position, any VEPs recorded from this jittered condition cannot result from local changes, and must therefore be generated by the alternation in stimulus polarity. In the following sections, the fundamental frequency of the contrast temporal modulation is simply referred to as temporal frequency and is measured in Hertz (cycles/s).

VEP recording

EEGs were recorded with surface electrodes (O_z, C_z, with Earth halfway between), preamplified 500-fold, filtered between 1-100 Hz, reamplified a further 100-fold, and connected to the A/D input (12 bits, AS-1 Cambridge Research System, Kent, UK) of a PC computer for real-time analysis. The computer

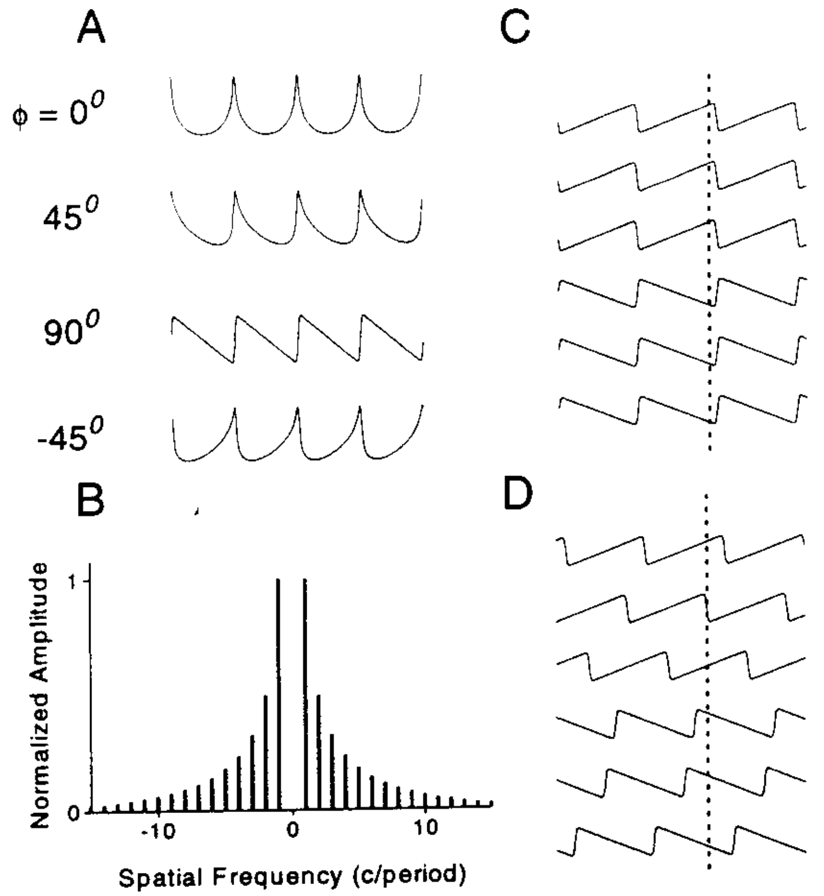

Fig. 1. A,B: Examples of the spatial profiles of the stimuli synthesized from eqn. (1) for four different values of the parameter ϕ. The amplitude spectrum of the stimuli is shown in B. Note that the profile for $\phi = 45$ deg and $\phi = -45$ deg are mirror symmetric. C,D: Schematic illustration of the display sequences of the stimulus. The sketches illustrate six consecutive temporal presentations for the steady (C) and jittered (D) conditions. In the steady condition, the stimulus remained in the same position while reversing in contrast periodically. In the jittered condition, it was moved to a new position at regular intervals, causing the luminance or the color at each spatial location to fluctuate randomly.

averaged the EEG in synchrony with stimulus contrast reversal, and calculated the amplitude and phase of the harmonics of the average signals by discrete Fourier analysis. To estimate background noise and artifacts, the computer also averaged online the EEG at a frequency 10% higher than the stimulation frequency (asynchronous noise), and calculated the amplitude and phase of the Fourier components of this average. Potentials whose amplitude were the same value of the background noise were considered unreliable. As an independent measure of reliability, we calculated the amplitude and phase of the second harmonic of individual "packets" of 40 sums, and derived an estimate of standard error from the two-dimensional scatter in amplitude and phase of the 40-sum packets (Victor & Mast, 1991). For details of the VEP recording techniques, see Morrone et al. (1993).

Five subjects with normal or well-corrected acuity and normal color vision (assessed by Ishihara tests) participated in these experiments. Visual evoked potentials were measured as function of color ratio, contrast, spatial phase, temporal frequency, spatial blur [σ of eqn. (2)], spatial frequency, and size of the stimulation field. For each subject the equiluminance point [r of eqn. (1)] was assessed independently by standard flicker photometry, and was always between 0.48 and 0.54. A total of 48 recording sessions were performed and in each recording session at least two complete sets of curves for the steady and the jittered condition were recorded. No major differences were observed between subjects. The results obtained as function of spatial blur, spatial frequency, and size of the viewing field will not be reported in detail for brevity of exposition.

Psychophysical thresholds

Thresholds were measured by a two-alternative-forced-choice procedure. For detection thresholds, the stimulus was presented in one of two successive intervals (each marked by a tone), which the observers had to identify by pressing the appropriate response buttons. The presentation was curtailed within a Gaussian envelope of time constant 400 ms, lasting 4 s in total. The contrast of the stimulus varied according to the QUEST (Watson & Pelli, 1983) procedure, which estimated threshold after each trial and placed the contrast of the following trial near the new estimate. For the discrimination thresholds, one interval contained a jittered bar or edge stimulus reversing in contrast or color at the appropriate temporal frequency, the other interval a jittered stimulus that alternated between a bar and an edge pattern at the same frequency. The subject had to determine in which interval the alternating from bar to edge stimulus was present. Four independent estimates of threshold were taken and the average reported.

Results

Previous work (Burr et al., 1992) has shown that sawtooth gratings that are jittered in space and periodically reversed in luminance contrast elicit a VEP response modulated in synchrony with the rate of inversion of polarity. Here we replicate this finding and extend it to color.

Fig. 2E shows an example of such a response to stimuli of luminance contrast, over two periods of modulation (four rever-

3.

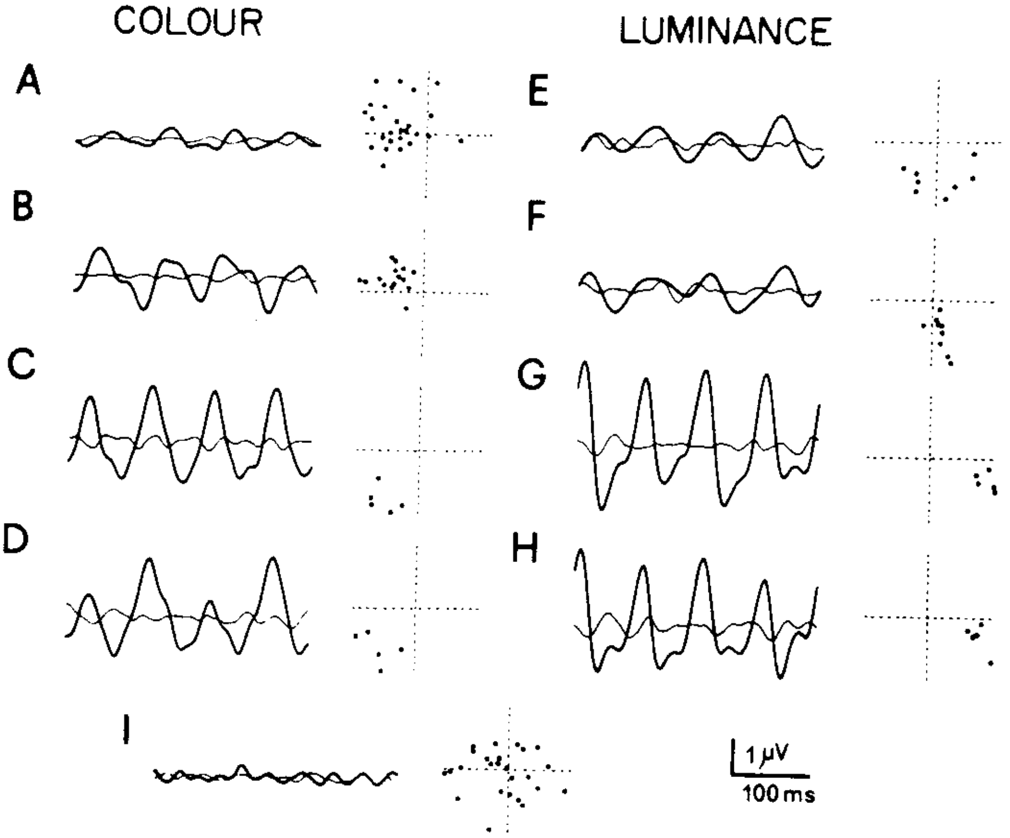

Fig. 2. Examples of VEPs from one subject (MCM) in response to edges (A, E, C, and G) and to bars (B, D, F, and H) for yellow-black luminance and red-green equiluminance stimuli (color ratio: $r = 0.5$). The first two rows show the VEP for the jittered condition, and the last two rows for the steady condition. The thick line shows the total average accumulated over two periods of stimulation (four reversals), and the thin line the average at an asynchronous frequency of 1.1 times the reversal frequency. Each dot of the polar plots shows the individual partial 40-sum response (note that the scale changes for the various polar plots). Temporal frequency of reversal was 6 Hz, jitter frequency 24 Hz, and fundamental spatial frequency 0.7 cycles/deg (14 cycles/screen). The power contrast for the equiluminant stimuli was 26%, for the luminance stimuli 7.3%. The panel in I shows the lack of response to a jittered stimulus (high contrast edges) so heavily filtered ($\sigma = 0.1$) as to resemble a sinusoidal grating. The amplitude, *S/N*, and ratio to the total power for the second harmonic modulation for the various records are:

	Amplitude (µV)	*S/N*	Power ratio (%)
A	0.34 ± 0.08	11	80
B	0.83 ± 0.09	11	46
C	1.8 ± 0.05	21	78
D	1.5 ± 0.2	9.2	63
E	0.5 ± 0.07	9	61
F	0.37 ± 0.07	7	40
G	2.3 ± 0.1	30	88
H	1.8 ± 0.2	10	71
I	0.07 ± 0.09	1.1	2

The Hotelling T^2 test reveals that the second-harmonic signal in A was significantly different from the response to the jittered sinusoidal grating in I ($P = 0.010$).

sals of contrast) at 6 Hz. As in the previous study, the bulk of the response occurred mainly at the second harmonic. The traces show four humps clearly distinct from the level of noise (thin line) evaluated from the asynchronous averaging of the EEG signal. A further indication of the reliability of the response is given by the polar plot to the right of the averaged traces, showing the amplitude and phase of the second harmonic of each partial (40-sum) average (see Methods). The degree to which the partial sums fall together is an indication of dispersion of the signal, and this can be used to estimate the error associated with the estimation of amplitude and phase (see Victor & Mast, 1991).

Reliable VEP responses can also be recorded from equiluminant jittered sawtooth stimuli (Fig. 2A), although the amplitudes are somewhat smaller. To be certain that the signal is reliable, and does not arise from artifact, we also measured VEPs to a heavily blurred sawtooth (amplified to keep the same peak-to-peak contrast). This stimulus was so blurred that there were essentially no higher harmonics that could give information about edge polarity. The response is shown in Fig. 2I. Note that the amplitude modulation is extremely low and that the individual packets span all of the four quadrants, producing an overall sum indistinguishable from noise.

The technique introduced by Burr et al. (1992) to study edge-specific responses (with sawtooth waveforms) can be readily extended to study bar-specific responses (with bar stimuli). The bars of this study had the same amplitude spectrum as the sawtooths (one the Hilbert transform of the other: see Fig. 1B). An example of responses to bar stimuli is reported in Figs. 2B and in 2F for stimuli of chromatic (equiluminant) and luminance contrast, respectively. As before the response is predominantly at the second harmonic. For stimuli of luminance contrast, the response to the bars is of similar amplitude to that to the sawtooth. For stimuli modulated in color, the bar response was twice that of the edge response. However, the phase of the bar response was very similar to that of the edge response, but both were clearly different from that for luminance contrast. This was a general finding and will be pursued more quantitatively later.

Figs. 2C, 2D, 2G, and 2H show the responses obtained when the same spatial stimuli were simply reversed in contrast ("steady" condition). As it is typically observed for standard VEPs (Fiorentini et al., 1991; Zemon et al., 1991; Morrone et al., 1993), the response phases for equiluminant stimuli were lagged compared with those for luminance modulation, in both the steady and jittered condition. However, all phases in the jitter condition are further shifted anticlockwise by about $\pi/4$ compared with the steady condition.

Color ratio

The dependence of the VEP response on color and luminance contrast can be studied by measuring the amplitude and phase of the response as a function of color ratio [r of eqn. (1) and indicated in the figures as $R/(R + G)$]. Fig. 3 shows the responses to edges and Fig. 4 the responses to bars, both for the same subject and the same temporal frequency (6 Hz). The two extreme points [$R/(R + G) = 0$ or 1] represent the response to stimuli of luminance contrast (green–black or red–black, respectively), and the central point the response to chromatic contrast [$R/(R + G) = 0.5$], corresponding to psychophysical equiluminance measured by standard flicker fusion photometry. Stimuli of intermediate color ratios contain various amounts of luminance and chromatic contrast.

The results obtained with the steady condition (Figs. 3A and 3B, Figs. 4A and 4B) show that the VEP amplitudes were largest for pure luminance contrast stimuli, and smallest for intermediate color ratios around 0.3 and 0.7, with a secondary peak at color ratio $r = 0.5$. The phases of the response also varied

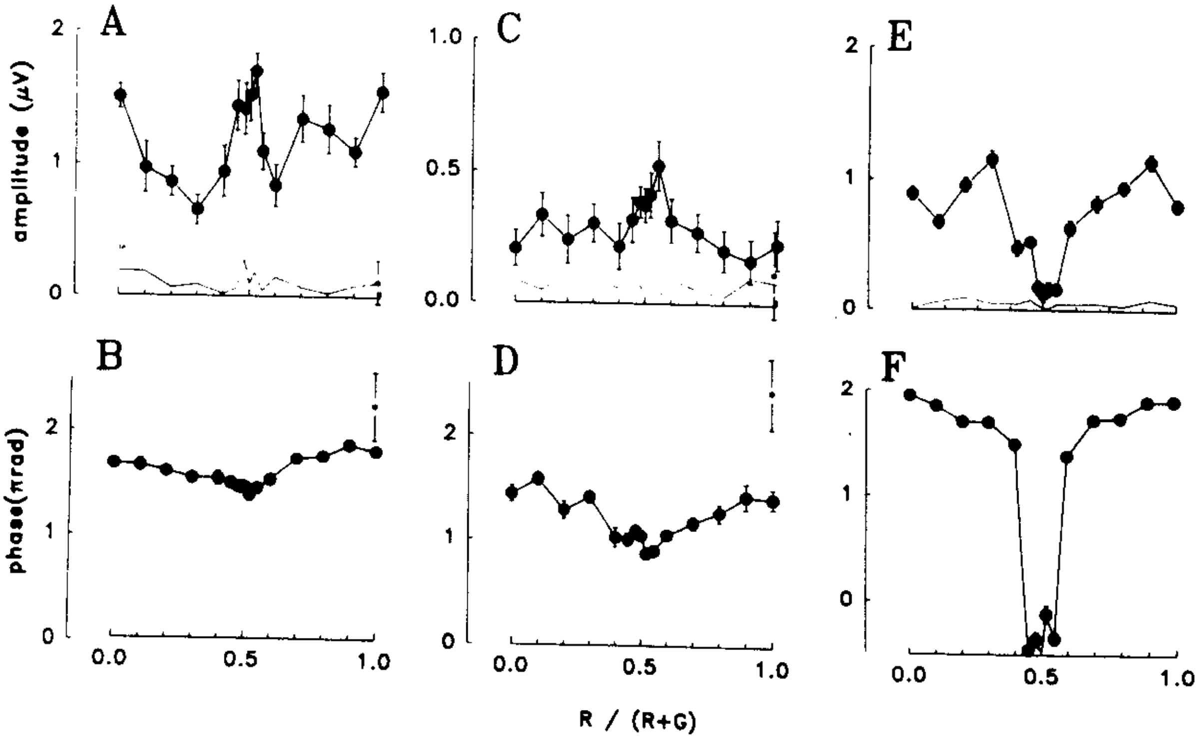

Fig. 3. Responses to edges reversed in polarity at the fundamental frequency of 6 Hz (12 reversal/s and 24 jitters/s), as a function of color ratio [$R/(R + G) = r$ of eqn. (1)] for MCM. The power contrast of the stimulus was 60%. Color ratios of 0 and 1 represent pure luminance green-black or red-black stimuli and a color ratio of 0.5 corresponds to the equiluminance point assessed by flicker photometry. The amplitude and phase of the second-harmonic modulation are shown in A and B for the steady condition, and in C and D for the jittered condition. E and F show the fourth-harmonic response, corresponding to the fundamental jitter frequency. Note that the position of the phases in F, near equiluminance, have been shifted by 2π to conform to the results in Fig. 4F. The dotted line shows the amplitude of the noise estimated by averaging at 1.1 times the reversal frequency. The stars show the amplitude and phase to a randomly jittering sinusoidal grating, which should evoke no polarity response.

5,

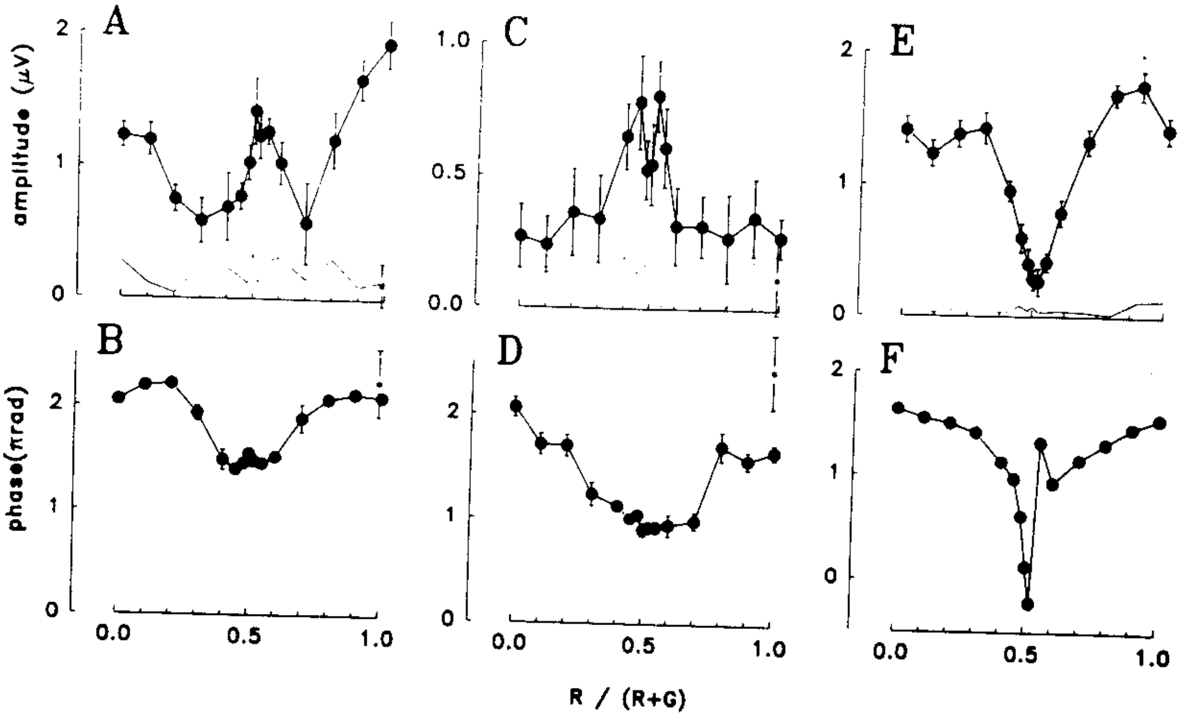

Fig. 4. Responses to bars reversed in polarity at 6 Hz as a function of color ratio for the subject MCM. The power contrast was 27%. Other conventions are as in Fig. 3.

systematically and symmetrically from the pure luminance to the pure chromatic contrast, being lagged by $2\pi/3-\pi/2$ at equiluminance.

In the jitter condition (Figs. 3C and 3D, Figs. 4C and 4D), where the response should be generated by edge-specific and bar-specific mechanisms (see Discussion), the response was also symmetrical about the equiluminant point, but here the amplitude was greater to color contrast than that to luminance contrast. Phases decreased steadily to a minimum at equiluminance, by a similar amount to that of the steady condition. If the phase difference is expressed as a difference in apparent latencies, the response to chromatic stimuli lags that to luminance stimuli by 35 ms, similar to the steady condition. However, the phases of both luminance and color of jittered condition are lagged with respect to the steady response, implying longer latencies.

Perhaps the most interesting aspect of Figs. 3 and 4 is the similarity of the responses to edges and to bars. The only difference is a slightly lower amplitude to the purely chromatic edges compared with purely chromatic bars in the jitter condition.

The color ratio to produce equiluminance for these subjects was 0.5 (measured by standard flicker fusion photometry), a value that corresponds well to the point of symmetry of the amplitude and phase curves. However, from the jitter results one can obtain a simultaneous estimate of equiluminance by measuring the response synchronized to the random jitter frequency. The jitter is at a high temporal frequency (24 jumps/s in this case), where the contribution of the color response should be weak (Kelly 1974; Burr & Morrone, 1993). The panels E and F of Figs. 3 and 4 show the amplitude and phases of the response at the jitter frequency. The amplitude plummeted to zero at psychophysical equiluminance (color ratio 0.5), with a sharp minimum in phase at nearby color ratios. This confirms that the point of symmetry and maximum amplitude of the response to edge or bar polarity inversion do correspond to the point of equiluminance, measured simultaneously for the same EEG signal.

Response curves as those shown in Figs. 3 and 4 were recorded for four subjects, and although the data varied somewhat in overall amplitude and overall phase offset from one subject to another, the general pattern of results (symmetric curves around the equiluminance point, maximum amplitude, and phase lag at equiluminance) were confirmed in all subjects. In one subject, the same experiment was repeated while restricting stimulated visual field to circles of 10 deg or 5 deg, yielding very similar results.

Dependence of responses on spatial phase of the stimulus

The edge and bar stimuli were synthesized from the same eqn. (1) with different values of the spatial phase of the stimulus: $\phi = 0$ defines a bar and $\phi = 90$ deg (or $\pi/2$) an edge. Varying ϕ between these two extremes generates a family of waveforms that can be considered to be a weighted sum of an edge and a bar. We recorded responses to stimuli of various spatial phases, keeping all of the other parameters constant. Fig. 5 shows the results of two subjects (PG: A and B; MCM: C and D), for luminance modulation (yellow-black, $r = 0.5$), color modulation (red-green, $r = 0.5$), steady and jittered conditions. To compare the response to chromatic contrast with that to luminance contrast, one should consider that the effective cone modulation produced by an equiluminant stimulus is less than that for luminance contrast, because of the overlap of the cone spectral functions. To allow for this, we reduced the contrast of the luminance stimuli for one subject (MCM) by a factor of 3.5 to

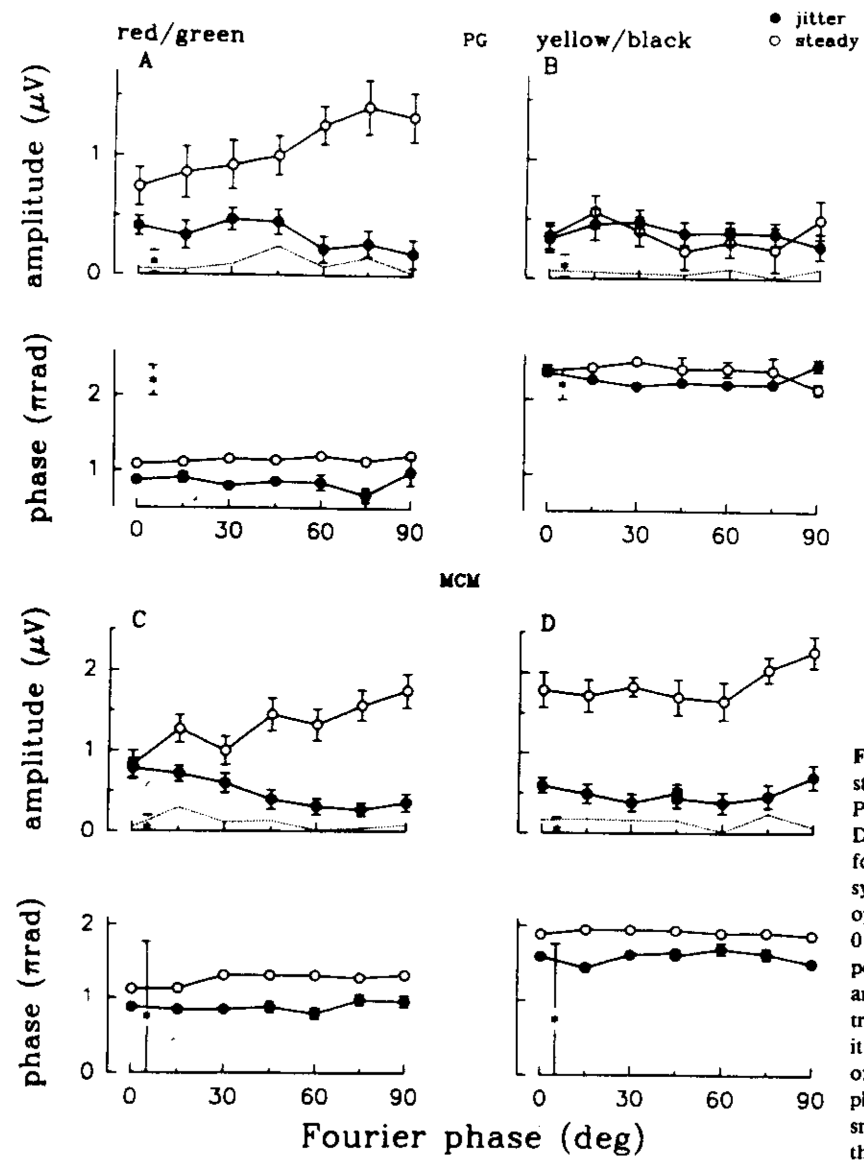

Fig. 5. Second-harmonic responses as a function of stimulus spatial phase [ϕ of eqn. (1)] for two subjects PG (top four panels) and MCM (bottom four panels). Data for chromatic contrast are on the left column, for luminance contrast on the right column. The filled symbols show the response to jittered stimuli and the open symbols to steady stimuli. A Fourier phase of 0 deg defines a bar, 90 deg an edge. The reversal temporal frequency was 6 Hz, the jitter frequency 24 Hz, and color ratio 0.5 for both subjects. The power contrast was 26% for all stimuli except for panel D where it was 7.2%. The dotted line and stars are estimates of the noise, as in previous figures. The response amplitudes to 90 deg equiluminant stimuli in A and C are small, but highly significant with S/N ratio greater than 7.

equate for cone contrast (rms cone contrast scaling factor 0.28, M cone contrast factor 0.37, L cone contrast factor 0.13). For the other observer (PG), the contrasts for both luminance and color were left at the maximal realizable value (26%).

Consider first the data for the jittered condition. For luminance stimuli, the response was practically independent of spatial phase. However, for the chromatic stimuli, the response to edges ($\phi = 90$ deg) was lower than for the bars, and changed smoothly between the two at intermediate Fourier phases. Although the VEPs to chromatic stimuli of $\phi = 90$ deg have low amplitude, the potentials were still highly reliable with S/N ratio higher than 7. The phases of the responses were constant under all conditions, indicating that the apparent delay was independent of the spatial phase of the stimulus.

For the steady condition, the response to luminance stimuli was again constant. The trend for chromatic stimuli was opposite to that of the jittered condition, with the response to bars being slightly lower than that to edges. The amplitude to luminance stimuli of subject PG was lower than for MCM, probably because of response saturation at the higher contrast.

Note the difference in phase between steady and jittered conditions and between the color and luminance contrast responses. Both differences are stable for the various stimuli and subjects, although more pronounced for PG, probably because of the higher contrast used for this subject for the luminance stimuli. It is unlikely that the difference in effective contrast of cone signals could explain this result, as the phase differences between chromatic and luminance contrast stimuli were also observed with subject MCM, where the cone contrast was equated for the two conditions.

Contrast response

The results so far show that at equiluminance it is possible to record responses specific to edge and bar polarity in the jitter condition, although the response to edges was always of lower amplitude. This may indicate a lower sensitivity to chromatic edges, or perhaps lower response gain. We explore these two possibilities by measuring the response to edge and bars as a

7.

function of contrast on three subjects. Fig. 6 shows a typical example of the pattern of the results.

All of the contrast response curves in the steady condition were very similar to those obtained for sinusoidal gratings at similar temporal frequencies (Fiorentini et al., 1991; Morrone et al., 1993) with amplitude decreasing more steeply for chromatic than for luminance contrast. The phases of both curves decreased steadily with decreasing contrast. For both luminance and chromatic stimuli, the contrast response curves to bar and edge were practically superimposed, despite the fact that the Michaelson contrast of the two patterns differed by about a factor of 2 for these stimuli. This suggests that the VEP response is directly related to the overall power (perhaps to the local energy: Morrone & Burr, 1988) of the stimuli, rather than to local Michaelson contrast.

The chromatic contrast response curves can be approximated by linear regression on semilogarithmic plots (up to response saturation). Extrapolation of the regression line to zero amplitude provides an estimate of threshold, that is usually in good agreement with the psychophysical estimate. The agreement holds for all range of stimulus temporal frequency, including very low frequency (lower than 1.5 Hz) that are unable to elicit reliable luminance contrast response (Fiorentini et al., 1991). The results of Fig. 6 show that similar results occurred with sawtooth and bar waveforms. The psychophysical detection thresholds (indicated by arrows) agree closely with the estimates obtained by extrapolation of VEP amplitudes to chromatic contrast (for detail of regression see figure caption). It is important to note that despite the relatively high temporal frequency used (6 Hz), the subject perceived the stimuli to be colored at detection threshold, suggesting that the threshold is mediated by chromatic opponent mechanisms (see Discussion).

The luminance contrast response curves usually have a more complex shape, comprising two or more different limbs with different slopes, often separated by local minima. The different limbs have been interpreted as reflecting activity of separate visual mechanisms, the magno and parvo pathways (Nakayama & Mackeben, 1982). For ramp and bar stimuli, the two limbs

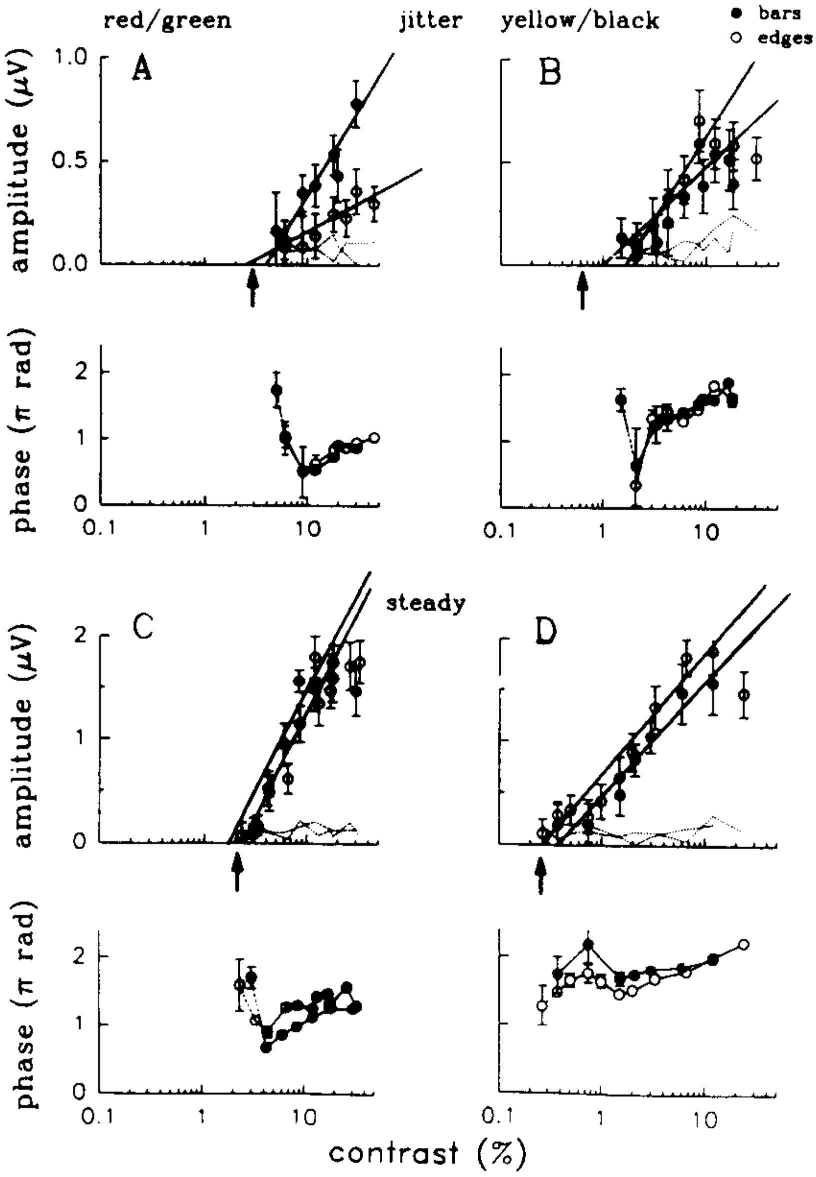

Fig. 6. Contrast response curves to bars (filled circles) and edges (open circles) reversed in luminance contrast (right) and in color contrast (left) at 6 Hz for subject MCM. Fundamental spatial frequency 0.7 cycles/deg, color ratio 0.5. The arrows show the psychophysical detection (C,D) and discrimination (A,B) thresholds (average of 4 Quest estimates). The straight lines are the best linear fit of the amplitude data negatively weighted with the S.E. of the amplitude estimate. Points near the noise level and those after response saturation were not used for the fit (but left in the figure). The short dashed lines join the phases of unreliable VEP (whose amplitude are equal to the background noise amplitude, shown by the dotted curves). The estimated threshold for the extrapolated VEP amplitude and the psychophysical measurements were:

	Stimulus	ψ	VEP	Excluded points contrast (%)
A	edge	2.9	2.6 (±0.4LU)	none
A	bar	2.9	4 (±0.2LU)	6,9
B	edge	0.62	1.5 (±0.155LU)	18,30
B	bar	0.62	1 (±0.2LU)	3.3,16,18
C	edge	2.0	2.7 (±0.04LU)	2.3,26,33
C	bar	2.1	1.7 (±0.14LU)	3,30
D	edge	0.26	0.26 (±0.07LU)	0.26,24
D	bar	0.23	0.36 (±0.15LU)	none

8.

are present in the response curves (Fig. 6D). However, they are not so clearly separated as in other conditions to allow a separate fitting for the estimation of contrast thresholds. When all of the data from the two limbs (except the saturated response at the highest edge contrast) were pooled together, the fitted linear curves still extrapolated very near to the psychophysical detection thresholds.

The pattern of results are basically the same for jittered luminance stimuli. There were no appreciable differences between the response to edges and/or bars at any contrast, and both extrapolate to a similar value (although there is some error associated with the extrapolation thresholds). With the jittered chromatic stimuli, the amplitudes to both bars and edges decreased linearly with contrast, but the response to the bar had higher *gain*. That is to say, the amplitude of response increased with contrast more rapidly than to the edge. Despite the difference in slope of the response curves, however, both curves extrapolated to a similar contrast, suggesting similar thresholds. The arrows in Figs. 6A and 6B show the psychophysical thresholds for discriminating a bar from an edge stimulus, when jittered and reversed at 6 Hz. Note that these discrimination thresholds agree reasonably well with the extrapolation of VEP data in all cases, and is particularly good for the stimuli modulated in color, suggesting a correlation between the bar- and/or edge-specific VEP signals and the phase-discrimination ability of the visual system.

Temporal frequency

The VEP response to chromatic stimuli is stronger at low than high temporal frequencies for sinusoidal temporal modulation (Fiorentini et al., 1991). Unfortunately, it was not possible to measure very low temporal frequencies with the jitter technique, since each reversal is necessarily abrupt therefore eliciting a transient type of response. The range of temporal frequencies between 5 and 6 Hz were chosen to be sufficiently low to elicit a strong chromatic contrast response while being high enough to avoid a spurious response to the third and higher harmonics of the abrupt polarity reversal (that should occur around 15–18 Hz, well above the optimal range for VEPs). However, to be certain that the results were not specific for the conditions reported here, we measured polarity-specific VEPs at several temporal frequencies, over at least a limited range.

Fig. 7 shows the response as a function of color ratio measured at 3.8 Hz for edges in the steady (A) and jitter conditions (B) for subject FR. At this temporal frequency, the relative response amplitude to stimuli modulated in luminance and color is different than at 6 Hz, but the curves as function of color ratio are still symmetrical about the equiluminance point. At equiluminance there is a local amplitude maximum in the jittered condition, and a lag in phase of about $\pi/3$ with respect to the luminance condition, corresponding to an apparent delay of about 22 ms.

Fig. 8 shows responses to bar stimuli reversed at the same rate (3.8 Hz) in the jitter condition for the same subject. Figs. 8A and 8C plot second-harmonic amplitude and phase, while Figs. 8B and 8D show the first-harmonic response. Fig. 8E shows the average VEP trace for two temporal periods of the equiluminant stimulus, with the corresponding polar plots for first (F) and second harmonic (G). It is obvious that at this temporal frequency much of the signal power is at the first harmonic, both for luminance and chromatic stimuli. The reliability of the first harmonic at equiluminance is shown by the clustering of the partial-sum packets of Fig. 8G. The presence of the first harmonic in the response to bars is not surprising given that the second-order statistics of the stimulus varies with bar polarity (which does not occur for the ramps: Victor, 1985; Victor &

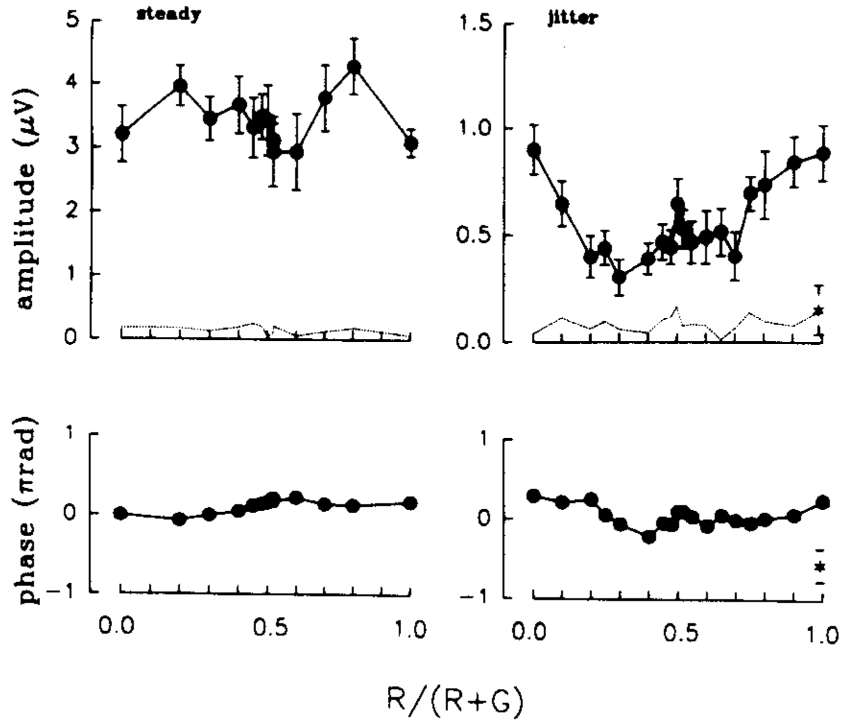

Fig. 7. Second-harmonic amplitude and phase of the response to edges (steady and jittered) as a function of color ratio for the subject FR. Polarity reversal 3.8 Hz; jitter frequency 30.4 Hz. Power contrast: 60%. Equiluminance color ratio 0.5. All other symbols are as in Fig. 3.

9.

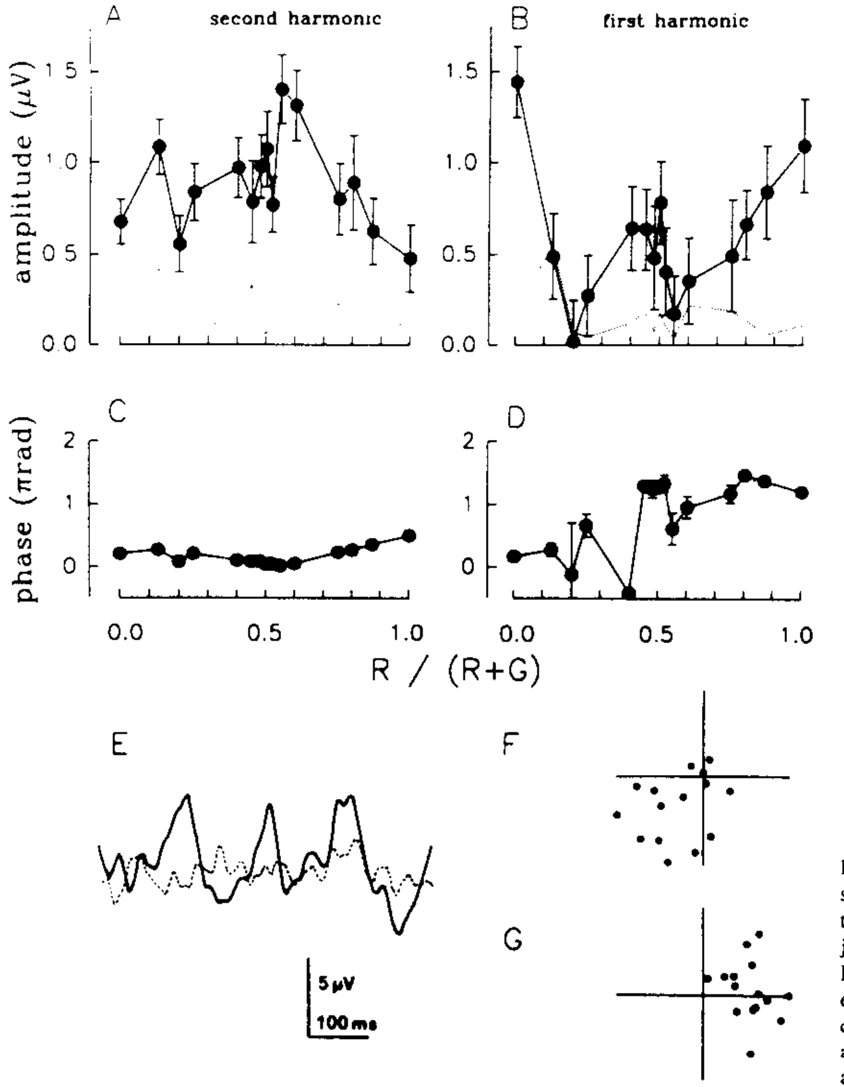

Fig. 8. Amplitude and phase of the first (B,D) and second-harmonic (A,C) components of the response to jittered bars as a function of color ratio for the subject FR. Polarity reversal 3.8 Hz; jitter frequency 30.4 Hz. Power contrast: 30%. The panel in E shows an example of a VEP trace for the color ratio of 0.5 accumulated over two periods of stimulation. Panels F and G show polar plots of partial averages for first and second harmonics, respectively.

Zemon, 1985). However, this does not affect the basic pattern of results for the second harmonic.

We were also able to record edge- and bar-specific responses at higher temporal frequencies, up to 9 Hz, and at temporal frequencies as low as 2 Hz (results not shown). However, at low frequencies (lower than 3.5 Hz) much of the power of the signal comes from the fourth and higher harmonics (that often coincide with the jitter frequency), so the analysis becomes complicated. Despite all of the technical constraints, we were able to replicate the basic results over a reasonably wide range of temporal frequencies, indicating that the effects were not peculiar to 6 Hz.

Discussion

We have demonstrated that reliable VEPs can be recorded in response to changes in the polarity of edge and bar modulation of both luminance and color contrast. The random jitter of the stimulus synchronized at a higher frequency than the reversal frequency ensured that the VEPs were generated by edge or line reversal, rather than by changes in local luminance or color.

The previous paper of Burr et al. (1992) discussed in detail how the VEP response to jittered ramp stimuli provides evidence for the existence of asymmetrical receptive fields. For the chromatic signal the reasoning is essentially the same. An equiluminant red-green ramp stimulus (a series of chromatic edges of the same sign) excites all types of chromatically opponent units, independently of the symmetry of their receptive fields. When the stimulus reverses in color contrast, all of these units will change their response. However, units with even-symmetric receptive fields will produce a mirror symmetrical response, preserving the parity of the input. Those units could therefore not contribute to the synchronized response, as the firing pattern does not change with the contrast alternation. If all chromatic neurons had even-symmetrical receptive fields, the VEP response to the ramp stimulus would not be modulated over time. Given that the response was strong and reliable over a large range of contrasts and other stimulus parameters, we must conclude that there exist chromatically opponent units with receptive fields that are not even-symmetric. A similar reasoning can be applied to the bar stimuli (showing that all units are not perfectly odd-symmetric) and to all of the other spatial phases. If only one class of receptive field existed with a specific phase spectrum, one would expect a null in the amplitude response for stimuli of certain spatial phases. However, the response as a function of stimulus phase varied by less than a factor of 2 in amplitude and was constant in phase for both luminance and chromatic stimuli, suggesting the existence of at least two different types of neurons with different phase spectra.

The exact type of symmetry of these neurons cannot be derived directly from the present data, nor can we be certain that there do not exist more than two types. For stimuli modulated in luminance, psychophysical experiments suggest the existence of mechanism with only even- and odd-field symmetry, at least for central vision. However, for peripheral stimuli, there appear to exist a range of field symmetries (Burr et al., 1989; Morrone et al., 1989). Similarly, electrophysiological studies have reported a range of receptive-field symmetries in the cat and monkey visual cortex (Field & Tolhurst, 1986; Hamilton et al., 1989). For color mechanisms, it is reasonable to assume the existence of chromatically opponent cells with even-symmetric receptive fields, given the ample evidence for these types of neurons from electrophysiological studies of primary and secondary visual cortex in monkey (Hubel & Wiesel, 1968; Livingstone & Hubel, 1984; T'so & Gilbert, 1988; Lennie et al., 1990). The lack of orientation selectivity of many cortical color opponent neurons is further evidence for receptive fields with even symmetry. On the other hand, very few studies have reported chromatically opponent cells with odd-symmetrical receptive fields (Michael, 1978*a–c*; Thorell et al. 1984), suggesting that they may be outnumbered by those with even-symmetric receptive fields. The greater response to the bar than to the edge stimuli, the gradual decrease of the response from the bar to the edge (Fig. 5), and the higher gain of the chromatic contrast response curve for the bar stimulus (Fig. 6) are all consistent with this suggestion. However, the similarity between the chromatic contrast sensitivity to bars and edges, evaluated by the extrapolation technique of the contrast response curves, would suggest that both even- and odd-symmetric receptive fields have similar sensitivity. Contrast thresholds are an index of the sensitivity of the mechanism, not of the overall numbers of units comprising the mechanism.

Contrast reversal of the bar pattern (but not the edge pattern) induces a change in the second-order statistics of the stimulus. Therefore, at least for luminance contrast, it is possible that the response could be generated by local nonlinearities that selectively amplify the response of one particular polarity (such as compressive luminance gain mechanisms) and hence not necessarily generated by mechanisms with particular symmetry. However, the data do not support this idea. The second-harmonic responses to jitter stimuli of all spatial phases were very similar both in amplitude and phase. Sawtooth and bar stimuli produced the same response for very low contrasts near the psychophysical discrimination threshold, reinforcing the suggestion that the responses to both stimuli arise from a subset of receptive fields with appropriate field symmetries. When the alternation rate was slower than 4 Hz, a first-harmonic component became apparent in the response. This component may arise from the different statistics of the pattern and to asymmetries in the ON and OFF pathways as it has been advocated by Zemon et al. (1988). Interestingly, the first-harmonic modulation also occurred for equiluminant stimuli and by analogy could be associated with asymmetry between the red and green center-opponent receptive field. However, this possibility should be viewed with some caution, given the recent psychophysical evidence for lack of asymmetry between the two populations of chromatic detectors, at least at threshold (De Marco et al., 1994).

The responses to the steady condition (Figs. 3 and 4) show many of the characteristics of the steady-state VEP to luminance and equiluminance sinusoidal gratings (Regan, 1973; Fiorentini et al., 1991; Morrone et al., 1993). For both VEPs and PERGs, amplitude curves tend to be symmetrical as a function of color ratio with a maximum or a minimum near the equiluminant point. The amplitude curves often have a W shape, with local minima flanking the maximum at equiluminance (Kulikowski et al., 1991; Morrone et al., 1993, 1994*a*,*b*). Previous studies have shown that this dependence on color ratio cannot be explained by chromatic units that linearly subtract the cone signals, such as L − M or S − (L + M). However, the responses to intermediate color-ratio stimuli can be well predicted by decomposing the physical stimulus into its luminance and chromatic contrast components and considering the separate VEP response to these components (for details see Morrone et al., 1993, 1994*a*,*b*; Morrone & Bedarida, 1995). The amplitude minima straddling the equiluminant point can be predicted by vector summation of the response to luminance and chromatic contrast, which are out-of-phase at these points. The result shows that the VEP response is strongly related to chromatic contrast and is not influenced by the average chromaticity of the stimulus.

Previous studies have suggested that the VEP response to contrast-reversed equiluminant stimuli reflects many of the properties of chromatically opponent units, over a wide range of stimulus parameters (Zemon et al., 1991; Fiorentini et al., 1991), although other stimulation paradigms may be equally effective (Murray et al., 1987). Nevertheless, some caution is still urged in interpreting VEPs to chromatic modulation. It is now clear from the electrophysiological literature that a reliable response of the magno cellular pathway can be elicited from equiluminant stimuli, both at retinal and cortical levels (Schiller & Colby, 1983; Lee et al., 1989; Saito et al., 1989; Gegenfurtner et al., 1994). This response is particularly strong at temporal frequencies around 10 Hz. It is therefore conceivable that the response to the jittered edge stimulus in equiluminance could be generated by achromatic units of the magno pathways. However, this interpretation is not supported by many results reported here. Although the magno pathway may respond at equiluminance, it does not convey any psychophysically useful information about the color of the stimulus (Merigan, 1991; Merigan & Mausell, 1993). For the psychophysical measurements reported here, subjects had to use color information to discriminate between a jittered bar and edge at equiluminance, and these psychophysical thresholds could be well predicted by extrapolating the VEP amplitude curves. The phases of the response to equiluminant bars and edges were always equal to each other, and quite different from the phase of the responses to stimuli modulated in luminance (even after equating for effective cone contrast). The response to jittered edge had local maxima at the equiluminant point, difficult to explain with a single population of M-type neurons that respond less vigorously to color than to luminance. Similar conclusions can be derived from the W-shape color-ratio response curves. It is hard to imagine how a spurious response from the achromatic magno pathways could produce these consistent results.

The amplitude of the VEP response to jittered stimuli of various contrasts extrapolates to values near the psychophysical threshold, with a particular good agreement for the equiluminant measurements. Note this is not a detection threshold but a discrimination threshold: the minimum contrast to distinguish a jittering series of lines from a jittering series of edges. The stimuli at this contrast, two to three times detection threshold, were all clearly visible and the judgment for the equiluminant patterns were based on the clearly visible spatial distribution of color. To our knowledge this is the first example of a VEP curve predicting discrimination performance. The good agreement of the prediction indicates that the recorded signal may be tapping those specific mechanisms that mediate spatial phase-discrimination tasks. Furthermore, the fact that the ratio between detection and discrimination thresholds was the same for the luminance and the equiluminance patterns suggests that phase discrimination for chromatic stimuli should be as good as for luminance stimuli. Measurements from our laboratory show that this is indeed the case, provided that multiharmonic stimuli are employed and that the contrasts of the luminance and chromatic stimuli are equated for detectability (Martini et al., 1993; Girard et al., 1993).

The second-harmonic component of the response to the "steady" (standard) condition was insensitive to the spatial phases of the stimulus: bars, edges, and weighted combinations of them eliciting the same second-harmonic response. In other words, stimuli that have the same overall spatio-temporal power produced the same VEP response, irrespective of its spatial profile. One way for this to occur would be for neuronal mechanisms to compute a "*local energy function*" of the input by squaring and summing the output of quasilinear units with odd- and even-symmetric receptive fields (Morrone & Burr, 1988). A model of this type would predict the same response for all of the family of stimuli used in this paper in the steady condition and also predict the same psychophysical thresholds for these stimuli. The present VEP data reinforces the idea that the generator of counterphase VEPs could be associated with the second-order nonlinearity of the "*local energy units.*" For the luminance system, many cortical units, such as the complex cell types, have property suitable to perform a local energy transformation. For the color system such units have not yet been described, but the present data would imply that they should exist.

One major difficulty in studying color vision is the possibility of artefactual responses arising from chromatic aberrations. The stimuli used here are broadband in spatial frequency, comprising harmonic components of up to 10 cycles/deg, that could be subject to chromatic aberration (Flitcroft, 1989). To minimize the problem, we blurred the stimuli with a Gaussian filter that heavily attenuated the contrast of the higher harmonics. Further consideration of the results rules out almost completely the likelihood of interference by chromatic aberrations. The response to steady-state stimulation produced very similar results to those obtained using very low spatial-frequency equiluminant sinusoidal gratings, that should be unaffected by chromatic aberration (compare the figures of this paper with those of Morrone et al., 1993; Fiorentini et al., 1991). In the jittered condition, we recorded simultaneously the response to the change of polarity and to jitter frequency. At equiluminance, the response to the reversal was maximum, while that to the jitter was absent, virtually excluding the possibility that the equiluminant response results from spurious luminance signals, that should be equally strong in both cases.

One important result is the phase lag of the chromatic response compared with the luminance response, both for the jittered and for the steady stimulation. The lag corresponds to a delay of about 30–40 ms for both conditions. This result confirms the electrophysiological reports of Fiorentini et al. (1991) and Regan and He (1993) that chromatic mechanisms have a longer integration time than luminance mechanisms. The VEP estimates also agree well with psychophysical demonstration of differences in response time for luminance and color stimuli, as estimated by reaction times (Nissen & Pokorny, 1977; Nissen et al., 1979), judgment of apparent simultaneity (Bowen, 1981) and summation (Swanson et al., 1987; Burr & Morrone, 1993). The difference in VEP delay between the response to stimuli modulated in color or luminance, on the other hand, is about 10–20 ms longer than that measured at the retinal level (Morrone et al., 1994*a*,*b*), indicating an involvement of thalamic or cortical mechanism in the integration time.

The response to jitter stimulation is also lagged with respect to the steady stimulation, by a similar amount for the color and luminance stimuli. In integration time the difference corresponds to about 20–30 ms, similar to that estimated by Burr et al. (1992). As discussed in that paper, the delay could reflect either the activity of a more sustained population of neurons generating the polarity specific VEP, or the activity of generators at a subsequent stage of visual processing. It is also interesting to note that all VEPs elicited by change in the structure of the pattern rather than change of local luminance have a latency that is usually longer than the characteristic 90–120 ms of transient pattern reversal response (Victor & Zemon, 1985; Bach & Meigen, 1992). Recent experiments in our laboratory show that also the latencies of orientation-specific VEPs (Braddick et al., 1986) is similar to those measured for the edge-specific VEP and texture segregation VEP, of about 140 ms. Although it is not possible to be more specific about the site of the generator, the longer latency and the agreement with the other studies indicate a clear involvement of cortical processing in the generator of the polarity-specific VEP, both for the color and the luminance response.

Having provided evidence for the existence of chromatically opponent units with a variety of spatial symmetries (including even- and odd-symmetrical receptive fields), it is reasonable to speculate about the functional significance of such neuronal machinery for color vision. Edges and bars are usually considered to be key features used to detect and perceive objects in a visual scene. A recent model (Morrone & Burr, 1988) suggests that feature detection can be achieved from the output of operators (mimicking human receptive fields) in quadrature phase. Any two particular phase spectra could be used, either the standard even- and odd-symmetric receptive-field pairs, corresponding to 0- and 90-deg phase spectrum, or any other phase spectra, such as 45 deg and −45 deg, corresponding to asymmetrical receptive fields. For achromatic vision, the local energy model has survived severe testing, and has been proven to predict quantitatively several visual phenomena (for review see Burr & Morrone, 1992, 1994). Preliminary results from our laboratory (Burr, 1993) show that the same tests used to validate the energy model for luminance scenes survive at equiluminance, suggesting that a similar strategy may be used by the color system. The results presented in this paper, demonstrating the existence of mechanisms with various phase spectra, give biological plausibility to the idea of an equivalent "local energy model" for color vision.

Acknowledgments

We are very grateful to David Burr for his critical and constructive help throughout this project and for fruitful discussions of the manuscript. We also thank Paolo Martini and Giulio Cappagli for competent technical help. Pascal Girard was supported by a Post-Doctoral fellowship from the "Science Program" of European Communities Commission.

References

Bach, M. & Meigen, T. (1992). Electrophysiological correlates of texture segregation in the human visual evoked potential. *Vision Research* **32**, 417–424.

Bowen, R.W. (1981). Latencies for chromatic and achromatic visual mechanisms. *Vision Research* **21**, 1457–1466.

Braddick, O.J., Wattam-Bell, J. & Atkinson, J. (1986). Orientation-specific responses develop in early infancy. *Nature* **320**, 617–619.

Burr, D.C. (1993). Visual representation of spatial phase. *Perception* **22S**, 30.

Burr, D.C. & Morrone, M.C. (1992). A non-linear model of feature detection. In *Non-Linear Vision*, ed. Pinter, R.B. & Nabet, B., pp. 309–328. New York: CRC Press, Inc.

Burr, D.C. & Morrone, M.C. (1993). Impulse response functions for chromatic and achromatic stimuli. *Journal of the Optical Society of America* **10**, 1706-1713.

Burr, D.C. & Morrone, M.C. (1994). The role of features in constructing visual images. In *Higher-Order Processing in the Visual System*, ed. Morgan, M.J. London: John Wiley.

Burr, D.C., Morrone, M.C. & Fiorentini, A. (1992). Electrophysiological investigation of edge-selective mechanisms of human vision. *Vision Research* **32**, 239–247.

Burr, D.C., Morrone, M.C. & Spinelli, D. (1989). Evidence for edge and bar detectors in human vision. *Vision Research* **29**, 419–431.

Canny, J. (1986). A computational approach to edge detection. *IEEE Transactions on Pattern Analysis and Machine Intelligence* **8**, 679–698.

DeMarco, P.J., Smith, V.C. & Pokorny, J. (1994). Effect of sawtooth polarity on chromatic and luminance detection. *Visual Neuroscience* **11**, 491–499.

Field, D.J. & Nachmias, J. (1984). Phase reversal discrimination. *Vision Research* **24**, 333–340.

Field, D.J. & Tolhurst, D.J. (1986). The structure and symmetry of simple-cell receptive-field profiles in the cat's visual cortex. *Proceedings of the Royal Society* (London) **228**, 379–400.

Fiorentini, A., Burr, D.C. & Morrone, M.C. (1991). Temporal characteristics of colour vision: VEP and Psychophysical measurements. In *From Pigments to Perception*, ed. Valberg, A. & Lee, B.B., pp. 139–150. New York: Plenum Press.

Flitcroft, D.I. (1989). The interactions between chromatic aberration, defocus and stimulus chromaticity: Implications for visual physiology and colorimetry. *Vision Research* **29**, 349–360.

Gegenfurtner, K.R., Kiper, D.C., Beusmans, J.M.H., Carandini, M., Zaidi, Q. & Movshon, J.A. (1994). Chromatic properties of neurons in macaque MT. *Visual Neuroscience* **11**, 455–466.

Girard, P., Martini, P., Morrone, M.C. & Burr, D. (1993). Electrophysiological and psychophysical investigation of phase sensitivity in human colour vision. *Investigative Ophthalmology and Visual Science* (Suppl.) **34**, 750.

Hamilton, D.B., Albrecht, D.G. & Geisler, W.S. (1989). Visual cortical receptive fields in monkey and cat: Spatial and temporal phase transfer function. *Vision Research* **29**, 1285–1308.

Hubel, D.H. & Wiesel, T.N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal Physiology* (London) **160**, 106–154.

Hubel, D.H. & Wiesel, T.N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal Physiology* (London) **195**, 215–243.

Jones, J.P. & Palmer, L.A. (1987). An evaluation of the two-dimensional gabor filter model of simple receptive fields in cat striate cortex. *Journal Neurophysiology* **58**, 1233–1258.

Kelly, D.H. (1974). Spatio-temporal frequency characteristics of color-vision mechanisms. *Journal of the Optical Society America* **64**, 983–990.

Kulikowski, J.J. & Bishop, P.O. (1981). Linear analysis of the responses of simple cells in the cat visual cortex. *Experimental Brain Research* **44**, 386–400.

Kulikowski, J.J. & King-Smith, P.E. (1973). Spatial arrangements of line, edges and grating detectors revealed by subthreshold summation. *Vision Research* **13**, 1455–1478.

Kulikowski, J.J., Murray, I.J. & Russel, M.H.A. (1991). Effect of stimulus size on chromatic and achromatic VEPs. In *Colour Vision Deficiencies X*, ed. Drum, B., Moreland, J.D. & Serra, A., pp. 51–56. Dordrecht: Kluwer Academic.

Lee, B.B., Martin, P.R., & Valberg, A. (1989). Nonlinear summation of M- and L-cone inputs to phasic retinal ganglion cells in the macaque. *Journal of Neuroscience* **9**, 1433–1442.

Lennie, P., Krauskopf, J. & Sclar, G. (1990). Chromatic mechanisms in striate cortex of macaque. *Journal of Neuroscience* **10**, 649–669.

Livingstone, M.S. & Hubel, D.H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience* **4**, 309–356.

Martini, P., Girard, P., Morrone, M.C. & Burr, D.C. (1993). Phase sensitivity is as good for chromatic as it is for luminance stimuli. *Perceptions* **22S**, 40.

Merigan, W.H. (1991). P and M pathway specialization in the macaque. In *From Pigments to Perception*, ed. Valberg, A. & Lee, B.B., pp. 117–126. New York: Plenum Press.

Merigan, W.H. & Maunsell, J.H.R. (1993). How parallel are the primate visual pathways? *Annual Review Neuroscience* **16**, 369–402.

Michael, C.R. (1978*a*). Color vision mechanisms in monkey striate cortex: Dual opponent cells with concentric receptive fields. *Journal of Neurophysiology* **41**, 572–588.

Michael, C.R. (1978*b*). Color vision mechanisms in monkey striate cortex: Simple cells with dual opponent color receptive fields. *Journal of Neurophysiology* **41**, 1233–1249.

Michael, C.R. (1978*c*). Color sensitive complex cells in monkey striate cortex. *Journal of Neurophysiology* **41**, 1250–1266.

Morrone, M.C. & Bedarida, L. (1995). A model of cone interaction for coding chromatic information. In *Colour Vision Research: Proceedings of the John Dalton Conference 9–13 September 1994*, ed. Kulikowski, J.J. London: Taylor and Francis (in press).

Morrone, M.C. & Burr, D.C. (1988). Feature detection in human vision: A phase dependent energy model. *Proceedings of the Royal Society B* (London) **235**, 221–245.

Morrone, M.C., Burr, D.C. & Fiorentini, A. (1993). Development of infant contrast sensitivity to chromatic stimuli. *Vision Research* **33**, 2535-2552.

Morrone, M.C., Burr, D.C. & Spinelli, D. (1989). Discrimination of spatial phase in central and peripheral vision. *Vision Research* **29**, 433–445.

Morrone, M.C., Fiorentini, A., Bisti, S., Porciatti, V. & Burr, D.C. (1994*a*). Pattern-reversal electroretinogram in response to chromatic stimuli: II. Monkey. *Visual Neuroscience* **11**, 873–884.

Morrone, M.C., Porciatti, V., Fiorentini, A. & Burr, D.C. (1994*b*). Pattern-reversal electroretinogram in response to chromatic stimuli: I. Humans. *Visual Neuroscience* **11**, 861–871.

Murray, I.J., Parry, N.R.A., Carden, D. & Kulikowski, J.J. (1987). Human visual evoked potentials to chromatic and achromatic gratings. *Clinical Visual Science* **1**, 231–244.

Nakayama, K. & Mackeben, M. (1982). Steady state visual evoked potentials in the alert primate. *Vision Research* **22**, 1261–1270.

Nissen, M.J. & Pokorny, J. (1977). Wavelength effects on simple reaction times. *Perception and Psychophysics* **22**, 457–462.

Nissen, M.J., Pokorny, J. & Smith, V. (1979). Chromatic information processing. *Journal of Experimental Psychology (Perception and Performance)* **5**, 406–419.

Pollen, D.A. & Ronner, S.F. (1981). Phase relationships between adjacent simple cells in the visual cortex. *Science* **212**, 1409–1411.

Regan, D. (1973). Evoked potentials specific to spatial patterns of luminance and colour. *Vision Research* **13**, 2381–2402.

Regan, D. & He, P. (1993). Magnetic brain responses to chromatic contrast in Human. *Investigative Ophthalmology and Visual Science* **34**, 794.

Saito, H., Tanaka, K., Isono, H., Yasuda, M. & Mikami, A. (1989). Directional selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Experimental Brain Research* **75**, 1–14.

Schiller, P.H. & Colby, C.L. (1983). The response of single cells in the lateral geniculate nucleus of the rhesus monkey to color and luminance contrast. *Vision Research* **23**, 1631–1641.

Smith, V.C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research* **15**, 161-171.

Swanson, W.H., Uneno, T., Smith, V.C. & Pokorny, J. (1987). Temporal modulation sensitivity and pulse-duration thresholds for chromatic and luminance perturbations. *Journal of the Optical Society America* **A4**, 1992-2005.

Thorell, L.G., DeValois, R.L. & Albrecht, D.G. (1984). Spatial mapping of monkey V1 cells with pure color and luminance stimuli. *Vision Research* **24**, 751-769.

Ts'o, D.Y. & Gilbert, C.D. (1988). The organisation of chromatic and spatial interactions in the primate striate cortex. *Journal Neuroscience* **8**, 1712-1727.

Victor, J.D. (1985). Complex visual textures as a tool for studying the VEP. *Vision Research* **25**, 1811-1827.

Victor, J.D. & Zemon, V. (1985). The human visual evoked potential: Analysis of components due to elementary and complex aspects of form. *Vision Research* **25**, 1829-1842.

Victor, J.D. & Mast, J. (1991). A new statistic for steady-state evoked potentials. *Electroencephalography and Clinical Neurology* **78**, 378-388.

Watson, A.B. & Pelli, D.G. (1983). QUEST: A Bayesian adaptive psychometric method. *Perception and Psychophysics* **33**, 113-120.

Zemon, V., Gordon, J. & Welch, J. (1988). Asymmetries in ON and OFF visual pathways of humans revealed using contrast-evoked cortical potentials. *Visual Neuroscience* **1**, 145-150.

Zemon, V., Siegfied, J. & Gordon, J. (1991). Magno and parvo pathways in humans studied using VEPs to luminance and chromatic contrast. *Investigative Ophthalmology and Visual Science* **32**, 1033.

14.