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CORTICAL CONTRAST GAIN CONTROL IN HUMAN SPATIAL VISION

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SUMMARY

1. We evaluated human visual cortical contrast gain using visual evoked potential (VEP) measurements. The steady-state VEP was elicited by 7·5 Hz contrast modulation of a 6 cycles/deg sinusoidal grating. The stimulus may be regarded as the sum of a steady grating ($\bar{C}$) and a counterphase grating of the same spatial frequency (ΔC). The counterphase grating is modulated sinusoidally in time.

2. The VEP was measured to combinations of different modulation contrasts (ΔC) and different mean levels of grating contrast ($\bar{C}$) which produced stimuli with contrast modulation depths ($\Delta C/C$) ranging from 0·0625 to 1·0 ('on–off').

3. The VEP signals were Fourier analysed and the amplitude and phase of the first (7·5 Hz) and second (15 Hz) harmonic frequency components were examined. The monocular VEP to a contrast-modulated grating contains significant first and second harmonic frequency components.

4. The amplitude and phase of the monocular VEP was plotted as a function of ΔC for each mean level of contrast explored. The amplitudes of both the first and second harmonic frequency components grow with increasing ΔC. However, the slope of each function depends on the mean contrast ($\bar{C}$): with higher levels of $\bar{C}$, the slope of the function is more shallow. Furthermore, at each level of $\bar{C}$ the amplitude of the first harmonic frequency saturates at a lower ΔC than does the second harmonic frequency component. VEP amplitude is therefore not determined by the absolute contrast change (ΔC) alone. The VEP phase of the first harmonic frequency shows less dependence on either modulation or on mean contrast; the phase of the second harmonic frequency component is strongly dependent on mean contrast ($\bar{C}$) but not on ΔC.

5. When the second harmonic amplitude component of the VEP response (R) is expressed as $R_{\text{actual}}/R_{\text{max}}$, where R_{max} is the response to $\bar{C} = \Delta C$ (i.e. 'on–off'), all second harmonic VEP functions can be well fitted with a power function. This is not the case for the function of the first harmonic amplitude data.

6. A dichoptic VEP was obtained by presenting the steady and counterphase

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gratings to opposite eyes. The dichoptic VEP, in distinction to the monocular VEP, contains only a second harmonic frequency component. The amplitude of the second harmonic frequency component grows with increasing ΔC, similar to the function seen for the monocular VEP. The phase of the dichoptic VEP shows a dependence on the mean contrast ($\bar{C}$) of the grating presented to the other eye, although the amount of phase change in the second harmonic frequency component of the VEP is less pronounced than that seen in the second harmonic frequency component of the monocular VEP.

7. The monocular *vs.* dichoptic data suggest that the origin of the first harmonic frequency component of the VEP (which occurs only with monocular stimulation) must arise at some point in the monocular pathway. The similarities between the second harmonic frequency component of the monocular and dichoptic VEP suggest, but do not establish, that the second harmonic frequency component of the monocular VEP is of cortical origin.

8. These data demonstrate that spatial contrast controls the gain of both the monocular and dichoptic visual evoked potential in the human.

INTRODUCTION

The effect of the average level of illumination on sensitivity to local changes in illumination has been studied extensively both in human psychophysics (Crawford, 1947; Baker, 1949; Rushton, 1962) and in primate electrophysiology (Boynton & Whitten, 1970). These sensitivity changes have been interpreted in terms of known properties of the photoreceptors. It is apparent however that neuronal signals from the distal retina onwards are also determined by differences in the illumination of adjacent retinal areas (i.e. by spatial contrast) (Shapley & Enroth-Cugell, 1984). Bodis-Wollner & Hendley (1979) used a contrast-modulated grating to explore the effect of mean contrast on the detection of contrast changes. This stimulus consists of a pattern whose deviation from the mean luminance is a product of a function of space and a function of time (see Fig. 1). The spatial function is a grating pattern with sinusoidal luminance profile and the temporal function is also a sinusoid. The contrast of the spatial function is modulated by the temporal function. Thus, as a result of temporal modulation, the spatial contrast changes between a peak and a minimum value, and contains a definite mean (average) contrast half-way between these two spatial contrast values. This stimulus can also be regarded as the sum of a steady and a temporally modulated counterphase grating of the same spatial frequency where the counterphase component produces the incremental and decremental contrast. A counterphase grating is a sinusoidally temporally modulated grating which changes its spatial phase through 180 deg during one temporal-modulating half-cycle. At peak contrast, the steady and counterphase gratings are in phase while at minimum contrast, they are out of phase (see Fig. 1). Bodis-Wollner & Hendley (1979) found that near threshold contrast, sensitivity to this modulated contrast is independent of mean contrast over a range of spatial frequencies. At suprathreshold contrast levels, however, and at high spatial frequencies, contrast modulation detection depends on mean contrast.

The effect of average contrast on the response to modulated contrast has also been

studied using electrophysiological recordings of visual evoked potentials (VEP) in humans (Bodis-Wollner, Hendley & Kulikowski, 1972). The stimulus was a sinusoidal grating with a spatial frequency of 6 cycles/deg of visual angle, which is near the peak of the contrast sensitivity function (Campbell & Green, 1965). That study showed that the amplitude of the VEP response is neither determined solely by the absolute level of contrast change (ΔC) nor by the contrast modulation depth (ratio of modulated contrast over average or steady contrast, $\Delta C/\bar{C}$).

The present VEP study re-evaluated the effect of mean contrast on modulated contrast taking a somewhat different approach. We wished to determine whether or not spatial contrast controls the gain of the human cortical response. We define contrast gain as the response (R) over a given change in contrast (ΔC), (gain = $R/\Delta C$). We evaluated whether or not the gain depends on average contrast. A contrast-modulated grating is a well-suited stimulus for this purpose. However, our earlier study (Bodis-Wollner *et al.* 1972) did not take into account the complexity of the VEP response to this type of stimulus. We subsequently found (Bodis-Wollner & Hendley, 1978), using Fourier analysis of the VEP waveform, that 'on–off' presentation of a grating (or a contrast modulation depth of 100%) produced a VEP consisting of significant first and second harmonic frequency components. For instance, using 8 Hz modulation frequency, the VEP will contain power at 8 Hz (first harmonic frequency) and at 16 Hz (second harmonic frequency).

While the amplitude functions of the two harmonic frequency components are parallel with increasing levels of mean contrast, the phase of only the second harmonic is contrast-dependent (Bobak, Bodis-Wollner, Harnois & Thornton, 1984). In the present study, therefore, the amplitude and phase functions of the different harmonic components of the contrast-modulated VEP were analysed separately to give a more complete picture. The present study shows that mean contrast controls the gain of the human cortical response over a range of modulation depths but this gain effect is expressed differently in the first and second harmonic components.

To examine the origin of contrast gain control in the visual pathway, we then compared the VEP response to monocular and dichoptic (steady grating in one eye and counterphase grating in opposite eye) presentation of the contrast-modulated grating. The results indicate that the first and second harmonic frequency components must originate from different sources.

Finally we examined contrast modulation curves specifically for levels of mean contrast centred around 10%. Recent studies have suggested that a contrast-dependent segregation of neurones exists in the primate visual pathway; the contrast sensitivity of cells in the magnocellular layers of the lateral geniculate nucleus is higher than that of the parvocellular layers. The contrast threshold appears to be near 10% in the parvocellular layers of the monkey (Shapley, Kaplan & Soodak, 1981; Kaplan & Shapley, 1982). We hoped that by using these particular levels of mean contrast, we may find some ensemble correlates to individual single-cell properties.

METHODS

Stimulus definitions

The spatial frequency of a grating pattern is expressed as the number of adjacent pairs of dark and bright bands subtending 1 deg of visual angle at the observer's eye.

The spatial contrast of a steady grating is generally defined as the difference of maximum (L_{max}) and minimum (L_{min}) luminance over their sum.

$$C = \frac{L_{max} - L_{min}}{L_{max} + L_{min}}. \quad (1)$$

In our study, contrast was temporally modulated. Thus L_{max} and L_{min} were not constant values. Therefore, in Fig. 1, we use L_1 for 'L_{max}' and L_2 for 'L_{min}' of the steady grating. The mean luminance therefore is

$$L = \frac{L_1 + L_2}{2}. \quad (2)$$

The spatial luminance profile of a sinusoidal grating is

$$L = \bar{L}(1 + C \cos 2\pi Fx), \quad (3)$$

where F = spatial frequency and x = distance horizontally. When the pattern is temporally modulated, its spatial contrast will change between a peak (C_{max}) and a minimum (C_{min}) contrast value. The difference in contrast between maximum and mean contrast as well as between mean and minimum contrast, we call ΔC. Bodis-Wollner *et al.* (1972) have shown that ΔC is proportional to ΔL. Thus

$$C = \bar{C} \pm \Delta C. \quad (4)$$

Therefore contrast modulation depth, M, may be defined as

$$M = \Delta C/\bar{C}, \text{ if and when } \bar{C} \neq 0. \quad (5)$$

Therefore the spatio-temporal luminance profile of our stimulus is described by

$$L(x,t) = \bar{L}[1 + C(t) \cos 2\pi Fx]. \quad (6)$$

when

$$C(t) = \bar{C} + \Delta C \cos \frac{\omega}{2\pi} t, \quad (7)$$

where C = contrast, $\bar{L}$ = mean luminance, F = spatial frequency, M = depth of modulation, x = distance horizontally, $C(t)$ = instantaneous contrast, $\omega/2\pi$ = temporal frequency in cycles per degree and $\bar{C}$ = mean contrast (Bodis-Wollner & Hendley, 1979). Figure 1 illustrates the luminance profile of a contrast-modulated grating in more detail.

Stimulus and apparatus

A 6 cycles/deg sinusoidal grating pattern was sinusoidally modulated in contrast about a mean level of contrast at 7·5 Hz.

Monocular viewing only. The grating was presented on a Joyce Electronics oscilloscope. The display subtended 9 deg at a viewing distance of 144 cm. Mean screen luminance was 141 cd²/m. The four mean levels of contrast were 0·275, 0·137, 0·097, and 0·049. The entire ΔC range in this study was from 0·0092 to 0·275. The ΔC range for each mean contrast, however, differed such that contrast modulation depth ($\Delta C/C$) ranged from 1 (or 100% modulation equalling an 'on–off pattern') to 0·05 depth of modulation. In these experiments no overmodulation was employed. The open eye viewed the display while the fellow eye was covered with a translucent patch.

Monocular and dichoptic viewing comparison. Rotated mirrors imaged the display of two Tektronix 608 monitors to each eye separately. Fusion was maintained by aligning fixation marks which were in the centre of each display screen. The displays subtended 8 deg at a viewing distance of 50 cm (5 cm from eye to mirror and 45 cm from mirror to screen). Mean screen luminance was 80 cd²/m. With monocular viewing, the contrast-modulated grating was presented to the right eye and a blank field of the same mean luminance to the left eye. With dichoptic viewing, a steady grating of a given mean contrast was presented to one eye and a counterphase grating of a given modulation contrast (ΔC) to the opposite eye. In some of these experiments, overmodulation ($\Delta C/\bar{C} > 1$) was employed, as shown in Fig. 1*e* and *f*. The mean contrast of the steady grating ranged from 0·275 to 0 (0 = no steady component, only a counterphase grating) with ΔC being constant either 0·048 or 0·069 for observer P. B. and 0·069 and 0·0975 for observer M. M.

VEP recording

VEPs were recorded with the active electrode at Z_5, the reference electrode at Z_{63}, and the forehead was grounded. 'Z' refers to the mid-line and the subscript, to the percentage of nasion-

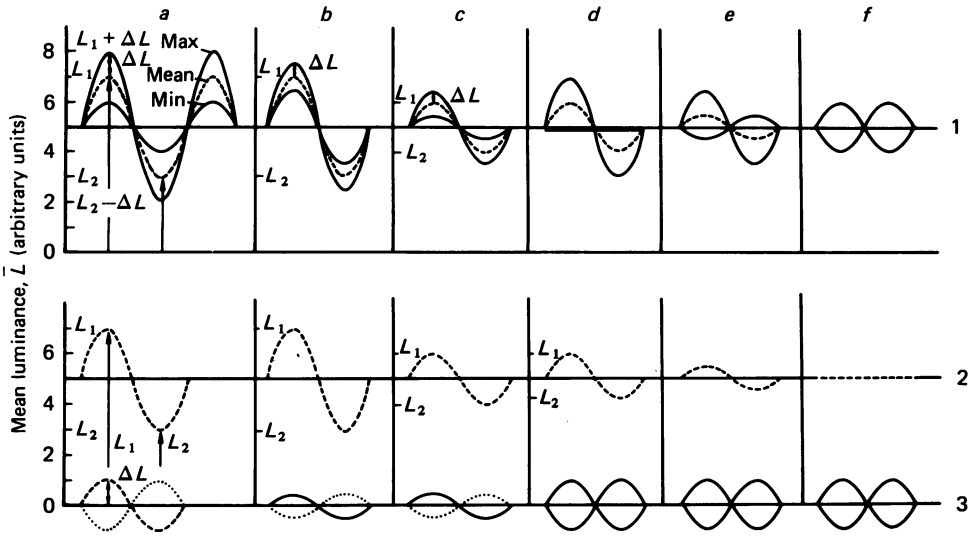

Fig. 1. Luminance profiles of modulated patterns used in this study. Notice that all patterns have the same mean luminance ($\bar{L} = L_1 - L_2/L_1 + L_2$) where L_1 refers to the peak and L_2 to the trough luminance of each unmodulated pattern. Row 1 shows profiles of temporally modulated patterns, row 2 represents the unmodulated pattern while the row 3 in each case represents a counterphase-modulated pattern, which needs to be summed with the steady pattern to produce the contrast-modulated pattern of row 1. *a*, the luminance profile of a contrast-modulated grating is shown on row 1 (*a*1). Max, the profile of the higher contrast state, which alternates with the lower contrast state (Min). The mean contrast profile is labelled as Mean, and is drawn using interrupted lines. The highest and lowest luminance levels of the individual bars which establish the mean contrast profile are labelled L_1 and L_2, respectively, and have values of 7 and 3 in *a* of this figure. Mean contrast is defined as $\bar{C} = (L_1 - L_2)/(L_1 + L_2)$. Thus, we can calculate that mean contrast is 0·4. Peak luminance values of the grating during modulation differ from the mean contrast profile by ΔL, which is therefore half the brightness change at the centre of each bar between the two contrast levels. By adding ΔL to L_1 and subtracting ΔL from L_2, contrast increases by ΔC. The converse decrease occurs when ΔL is subtracted from L_1 and added to L_2. Modulation depth is given by $\Delta C/\bar{C}$, and it is 0·5. This means that the maximum contrast is 50% higher and the minimum contrast is 50% lower than the mean contrast. Notice that ΔC is 0·2. The contrast-modulated grating can alternatively be viewed as the sum of a steady grating (*a*2), and a 'counterphase flicker' grating (*a*3), which alternates between two symmetrical states that are 180 deg spatially out of phase, and consequently has no standing contrast. *b*, row 1 shows a smaller modulation depth at the same mean contrast as in *a*. Note that the steady component (*b*2) of this contrast-modulated grating has the same amplitude as in *a*2. In the *b* column, a mean contrast of 0·4 is modulated with a modulation depth of 0·25, so that $\Delta C = 0{\cdot}1$. Thus, *a*2 = *b*2 although the counterphase component (*b*3) has half the amplitude of *a*3. *c*, section *c*1 shows a lower mean contrast (0·2) at the same modulation depth (0·5) as in *a*. Notice that $\Delta C = 0{\cdot}1$ as in *b*. In other words, the steady component, *c*2, has half the amplitude of *a*2 or *b*2 while the counterphase component, *c*3, has the same amplitude as *b*3 and half that of *a*3. *d*, section *d*1 has mean contrast of 0·2, as in section *c*. $\Delta L = L_1 - \bar{L}$, which means that the modulated pattern appears and disappears in the following manner: contrast is 0·4 at its maximum and 0 at its minimum. *e*, section *e*1 shows a mean contrast of 0·1; however, the modulated (counterphase, *e*3) component has the same value as in *a*3 and *d*3. This results in 'over-modulation' as shown in *e*1. *f*, section *f*1 has the mean contrast reduced to 0, while the counterphase component remains the same as in *a*3, *d*3 and *e*3. This results in a pure counterphase pattern. As explained in the Results section, adding a steady grating to a simple counterphase stimulus (as shown in *e*) can *increase* the VEP amplitude.

to-inion distance. Signals were amplified with a Grass P511 pre-amplifier with bandpass half-amplitude settings at 3 Hz (low) and 100 Hz (high). After amplification, signals were fed into a PDP 11/23 microcomputer which averaged four 30 s response periods for each experimental condition.

VEP response analysis

The amplitude and phase of the first and second harmonic components in the VEP response were determined with PDP 11/23 Fourier analysis software (Milkman, Schick, Rosetto, Ratliff, Shapley & Victor, 1980). Amplitude was expressed as half of the peak-to-trough voltage. The bandwidth of each spectral component was 0·03 Hz. Higher odd and even harmonics were present but not analysed as the amplitudes were small with a poor signal-to-noise ratio. The 'noise' estimate was based on the VEP response obtained while viewing an unmodulated blank screen of the same mean luminance.

Observers

Four observers (age range, 18–30 years) participated once in all experimental conditions in which only monocular viewing was used. Monocular and dichoptic viewing comparisons were obtained in two of these observers with four replications per experimental condition over separate days. All observers had 20/20 acuity with no visual complaints.

Procedure

In conditions where only monocular viewing was used, one mean contrast ($\bar{C}$) was presented within a testing session with levels of ΔC being randomized. With the dichoptic and monocular viewing comparison, ΔC was constant within a testing session with random presentation of mean contrast level and monocular *vs.* dichoptic viewing condition.

Calibrations

The luminance of the cathode ray tube (CRT) was measured by a SEI photometer. A linear photodiode tube (RCA 5583) was firmly positioned in front of the CRT. Between the photocell and the CRT two vertical slits were positioned behind each other. This double-slit aperture ensured that the photocell sampled only input to about 2 mm of the screen of the CRT. The output voltage of the photodiode was measured and the contrast was calculated from these readings (Bodis-Wollner & Hendley, 1979), as detailed below. This procedure was followed for the Joyce oscilloscope and for the two Tektronix monitors.

Contrast versus Z-axis input voltage

Measurements were taken over a stationary grating by shifting the grating behind the slit for maximum and minimum output of the photocell. The amplitude of the carrier was changed in 3 dB (0·15 log unit steps) from 4 to 60 V. The contrast increased linearly up to 0·50 on the Tektronix scopes and up to at least 0·80 on the Joyce oscilloscope.

Measurements were taken over the bright band of the grating by finding the position of maximum output. The counterphase modulation was applied to the carrier and both the maximum and minimum luminance were measured without repositioning either the photocell or the grating.

Measurements were taken over the bright band and then, by repositioning the grating, over the dark band of the unmodulated grating in the range between 0·04 and 0·40 mean contrast. In each position, 7·5 Hz contrast modulation was applied up to a maximum contrast of 0·55. The measured contrast increased linearly with voltage and coincided with the calculated contrast up to 0·50 regardless of which of these calibration methods was used.

RESULTS

The mean contrast of a contrast-modulated grating affects the amplitude and phase characteristics of the VEP. In all observers, the VEP contained first and second harmonic frequency responses as the major components. After a discussion of the replicability of the data, results obtained with monocular grating presentation

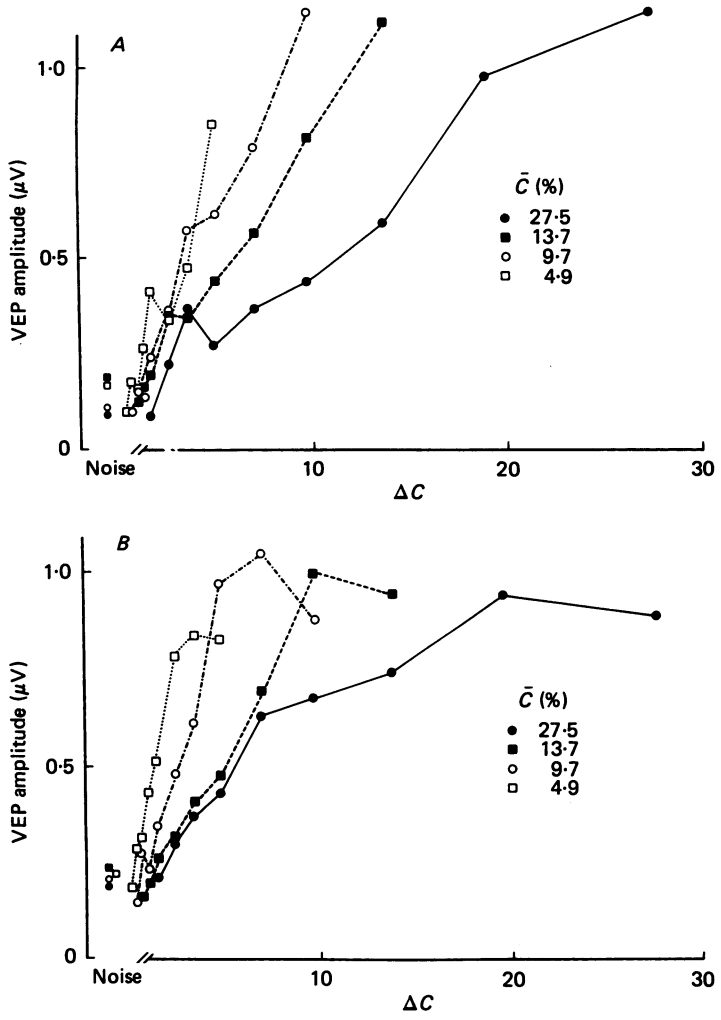

Fig. 2. Mean VEP amplitude data of four observers as a function of ΔC for each level of mean contrast ($\bar{C}$). The contrast-modulated grating was presented monocularly. The first harmonic results are shown in *A* and the second harmonic in *B*. Our VEP noise estimate was obtained by viewing a 'blank' screen (lower left of each panel) as explained in the text. Note that for a given ΔC, VEP amplitude is not constant but varies with an apparent orderliness depending on mean contrast.

will be described and then followed by a description of results obtained with dichoptic presentation.

Replicability of VEP data

As mentioned earlier, four replications for each experimental condition were obtained in two observers. Phase data between testing sessions showed little variability; amplitude was more variable. The separation between S.E.M. bars shown in Figs 5, 6 and 7 and the similarity of data trends between observers, however, indicate the validity of the major experimental results which will be discussed.

The VEP as a function of ΔC

By measuring the averaged VEP traces which probably represented the summed first and higher harmonic frequency components, Bodis-Wollner *et al.* (1972) found that VEP amplitude to a 6 cycles/deg contrast-modulated grating was not determined solely by the absolute level of contrast change (ΔC) but depended also on mean contrast ($\bar{C}$). Stated differently, the VEP amplitude to a counterphase grating is influenced by the mean contrast of the steady grating. Figure 2 demonstrates that this remains true even when each harmonic component is separately analysed; VEP amplitude for a given ΔC is not constant across different levels of mean contrast.

TABLE 1. Linear regression summary for VEP amplitude as a function of ΔC in Fig. 2

Mean contrast (%)	Slope	Y-intercept	Correlation
		First harmonic	
4·9	0·30	0·05	0·67**
9·7	0·19	0·01	0·69**
13·7	0·09	0·08	0·60**
27·5	0·08	0·06	0·60**
		Second harmonic	
4·9	0·21	−0·21	0·85**
9·7	0·11	0·05	0·53*
13·7	0·07	0·08	0·64**
27·5	0·04	0·08	0·70**

Regression lines are fitted only to the linear portion of each mean contrast curve. For the second harmonic, therefore, curves start at the highest ΔC for each level of mean contrast while for the first harmonic, curves start at a lower ΔC value, before VEP amplitude saturation. Each regression line equation is based on four VEP amplitude readings for each level of ΔC, one reading for each of the four observers. *$P < 0{\cdot}05$; **$P < 0{\cdot}001$.

Rather, VEP amplitude as a function of ΔC is dependent on $\bar{C}$. The slope of the amplitude function expressed in this way is shallower for higher mean contrasts. Therefore, the results presented in Fig. 2 and in Table 1 (see below) suggest that response gain depends on mean contrast.

Although the amplitude functions of both harmonic components grow with ΔC, there are differences between them. The amplitude of the first harmonic frequency component saturates at a lower ΔC than that of the second harmonic frequency component. This raises the possibility that the second harmonic frequency response arises from a saturating non-linearity of the first harmonic response. This is not likely, however. Inspection of Fig. 2 reveals that the 'take-off' of the second harmonic response is much below the saturating point of the corresponding first harmonic frequency curve. Furthermore, there is no slope change occurring in the second harmonic curve at the point where the first harmonic saturates. And finally, the slopes are different.

A major difference between the first and second harmonic components is also revealed by the respective slopes of their functions. At each level of mean contrast, the slope of the function relating VEP amplitude to ΔC is steeper for the first than for the second harmonic frequency component. These data are summarized in Table 1.

There are also differences in the phase characteristics of the first and second harmonic frequency components to contrast modulation. We reported earlier that with 'on–off' gratings or a contrast modulation depth of 100%, the phase of the second harmonic changes more steeply with increasing mean contrast than that of the first harmonic (Bobak *et al.* 1984). The present study confirms this over a range

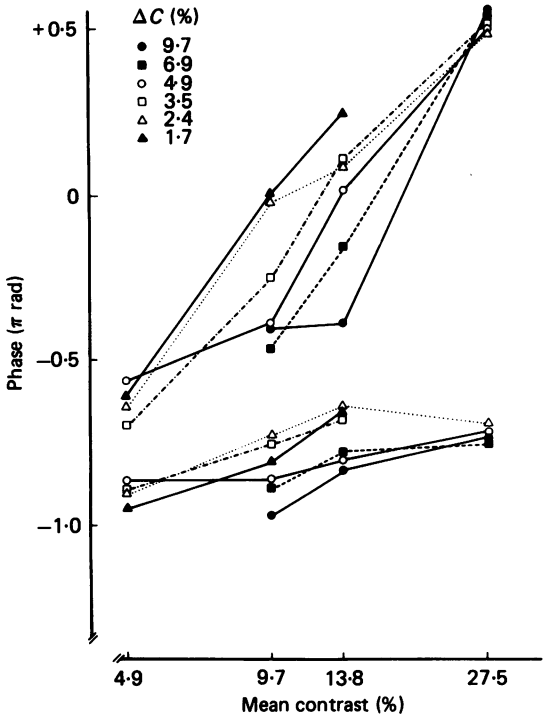

Fig. 3. Mean VEP phase data of four observers as a function of mean contrast for each level of modulation contrast (ΔC). Monocular grating presentation was used. First harmonic results are shown on the bottom, second harmonic results on the top.

of modulation depths. In Fig. 3, it can be seen that the phase of the first harmonic changes little as a function of mean or modulated contrast. The phase of the second harmonic, however, is strongly dependent on mean contrast: the phase change for a given ΔC is greater with the lower $\bar{C}$.

The VEP as a function of modulation depth ($\Delta C/\bar{C}$)

We have just demonstrated that the amplitude and phase of both major VEP harmonic frequency components are not determined by the absolute level of contrast change (ΔC); the response to an equal increment or decrement in contrast clearly varies with mean contrast. One way to represent the relationship between mean and modulated contrast is by plotting the response as a function of contrast modulation depth ($\Delta C/\bar{C}$).

To examine the quantitative relationship between VEP amplitude and contrast modulation depth, the VEP amplitude at 100% modulation depth (in Fig. 2) was defined as the maximum obtainable response (R_{max}) given the constraints of our

study. We then normalized the response at each modulation depth to this experimentally defined R_{max}. Figure 4 demonstrates that when VEP amplitude is expressed in this normalized fashion (percentage of the maximum response at each level of mean contrast) the data of the second harmonic frequency component (reported in Fig. 2) show a lawful trend. There is a convincing power relationship between response amplitude and modulation depth as indicated by the perfect linear fit on log–log co-ordinates. The exponent (A) which is the slope of the power function is nearly equal for the second harmonic at all tested levels of mean contrast ($\bar{C}$ = 0·275, A = 0·831; $\bar{C}$ = 0·14, A = 0·77; $\bar{C}$ = 0·10, A = 0·87; and $\bar{C}$ = 0·049, A = 0·89).

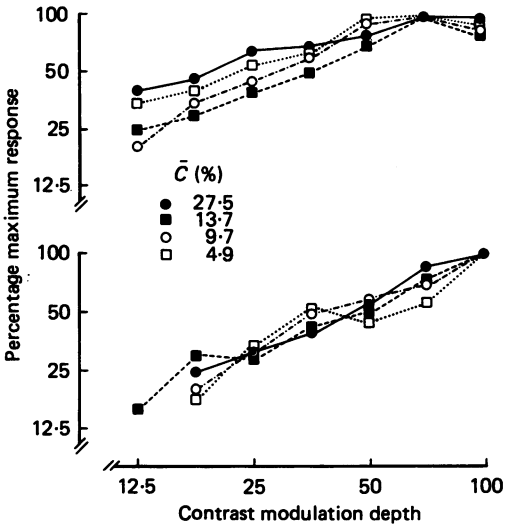

Fig. 4. Relative VEP amplitude (from Fig. 2) as a function of contrast modulation depth ($\Delta C/C$) for the first harmonic (top) and the second harmonic (bottom) VEP component (note log–log axes). Contrast modulation depth was varied in 0·15 log unit steps for each level of $\bar{C}$ and ranged from 100% ('on–off' pattern) to 12·5%.

This result indicates that VEP amplitude as a function of modulation depth is not only controlled by mean contrast but that the second harmonic frequency amplitude is uniformly scaled across levels of mean contrast. When the first harmonic frequency data are normalized in this fashion, the results obtained at different levels of mean contrast fall further apart from a single regression line. We are not confident of an exponential fit to the obtained first harmonic frequency curves.

Dichoptic contrast modulation curves

We used dichoptic viewing of a contrast-modulated grating to localize the source of the effects just described with monocular presentation. In this experiment, a steady grating was presented to one eye and a counterphase grating to the opposite eye, as described in the Methods section. We found that with such a presentation, the VEP response contains only a second harmonic frequency component. The first harmonic frequency component yields unreliable phase measurements and the amplitude values are below the 'noise' level. Therefore, the first harmonic frequency

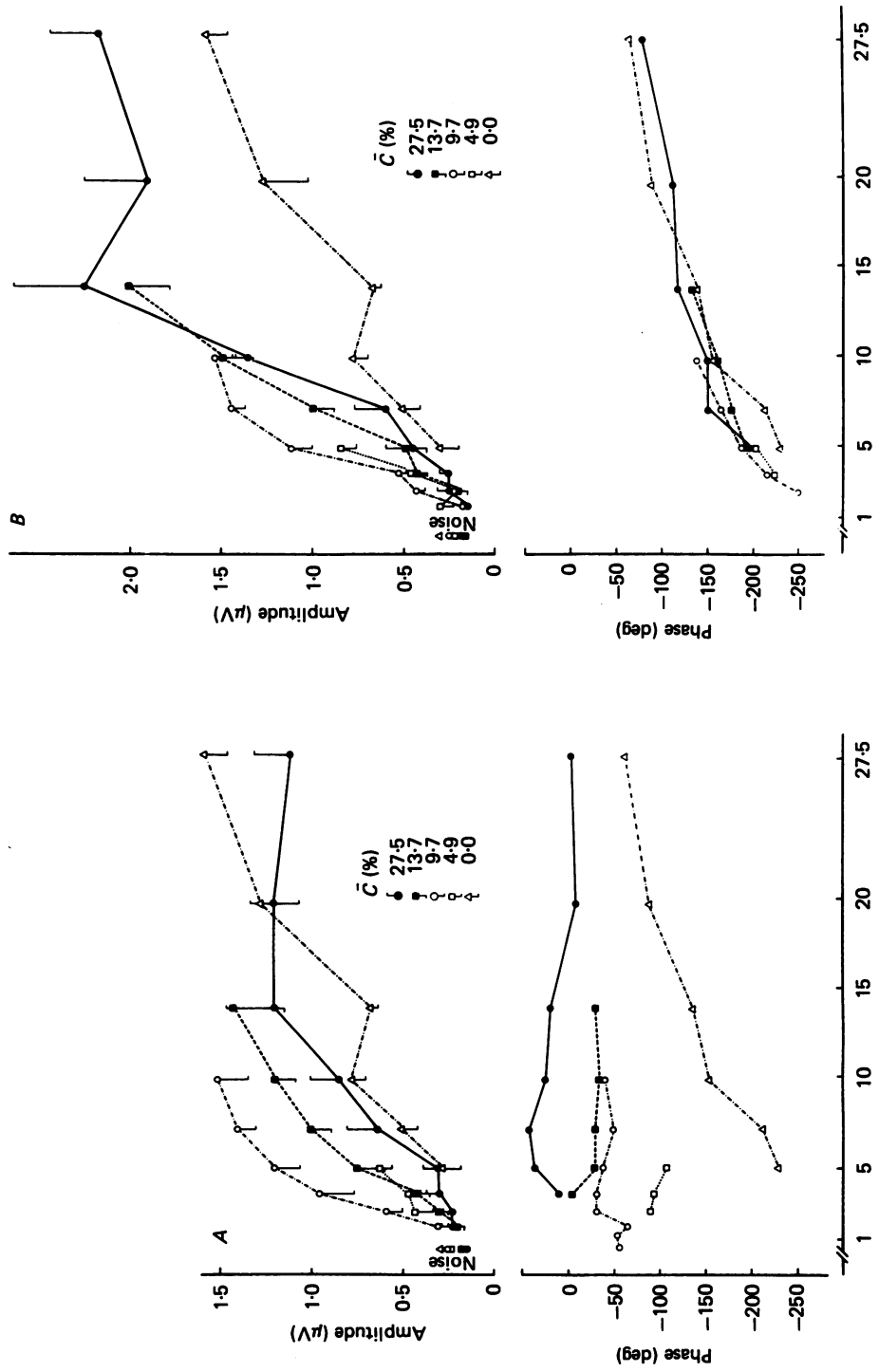

Fig. 5. The second harmonic amplitude and phase are shown as functions of ΔC in a single observer (P. B.) for monocular (*A*) and dichoptic (*B*) presentation of different levels of mean contrast. Each point is the mean of four replications with vertical bars representing + 1 S.E.M. A mean contrast of 0 represents counterphase presentation of the grating at the corresponding modulation contrast. S.E.M. bars are not shown for phase data as variability between testing sessions was extremely small, within degrees for each experimental condition.

is most likely generated in monocular pathways. The second harmonic amplitude functions are similar for dichoptic and monocular conditions. Figure 5 compares the monocular and dichoptic second harmonic frequency responses of a single observer to the same contrast modulation conditions as in Fig. 2. There are several noteworthy findings. First, the amplitude of the second harmonic to a contrast-

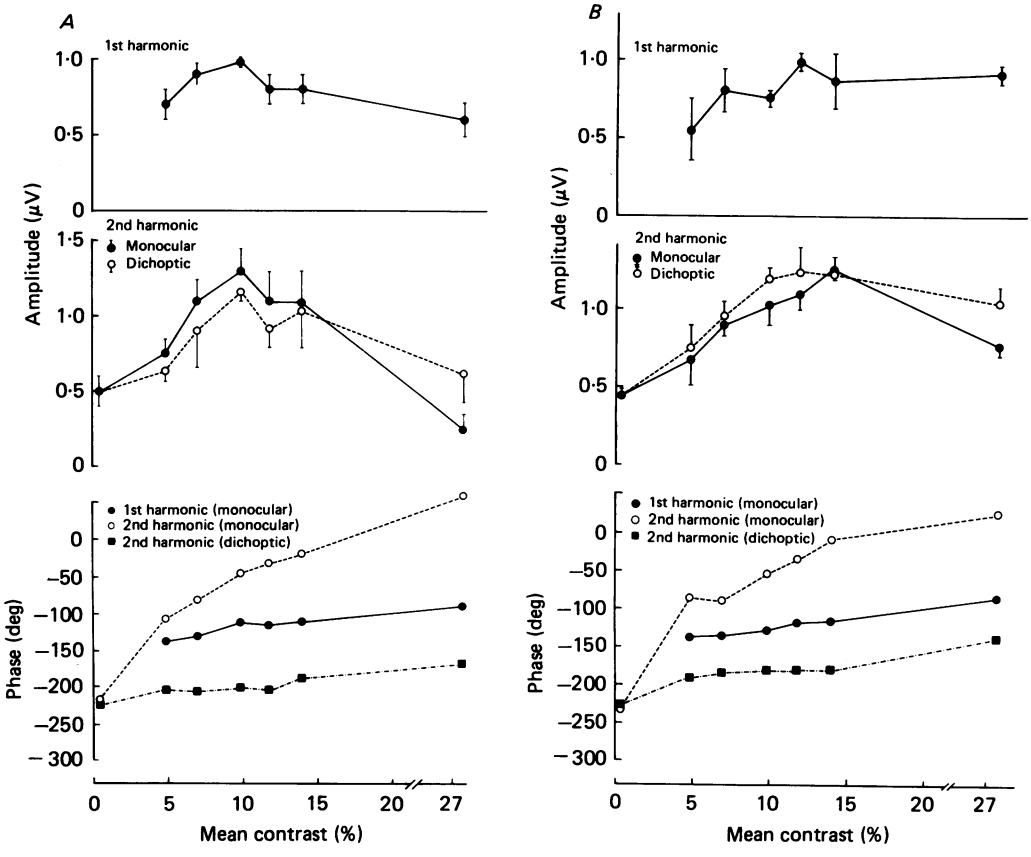

Fig. 6. VEP response functions are compared for monocular and dichoptic grating presentation for observer P. B. VEP amplitude and phase are shown as functions of mean contrast for modulation contrasts of 4·8% (*A*) and 6·9% (*B*). Again, a mean contrast of 0 represents counterphase presentation of the grating at the corresponding modulation contrast. Each data point is the mean of four replications with vertical bars in the amplitude function representing + 1 S.E.M. S.E.M. bars are not shown for the phase data as variability between testing sessions was small, within degrees for each experimental condition. Note that overmodulation occurs for mean contrasts less than ΔC.

modulated grating can be greater than the amplitude to a counterphase grating of the same contrast (i.e. mean contrast of zero). This result is inconsistent with the possibility that the decrease in VEP amplitude found with increasing levels of mean contrast is simply a masking effect or fatigue in which the response to modulated contrast is suppressed with high levels of mean contrast. A similar conclusion was reached by Spekreijse, van der Tweel & Zuidema, (1973) with transient VEPs to a

modulated checkerboard stimulus. A second point concerns the origin of the second harmonic frequency component arising from dichoptic presentation of the contrast-modulated grating. The presence of this response with dichoptic presentation suggests that the second harmonic frequency component originates at or beyond binocular cortical neurones. The VEP phase of the second harmonic frequency, however, shows less change as a function of mean contrast with dichoptic than with

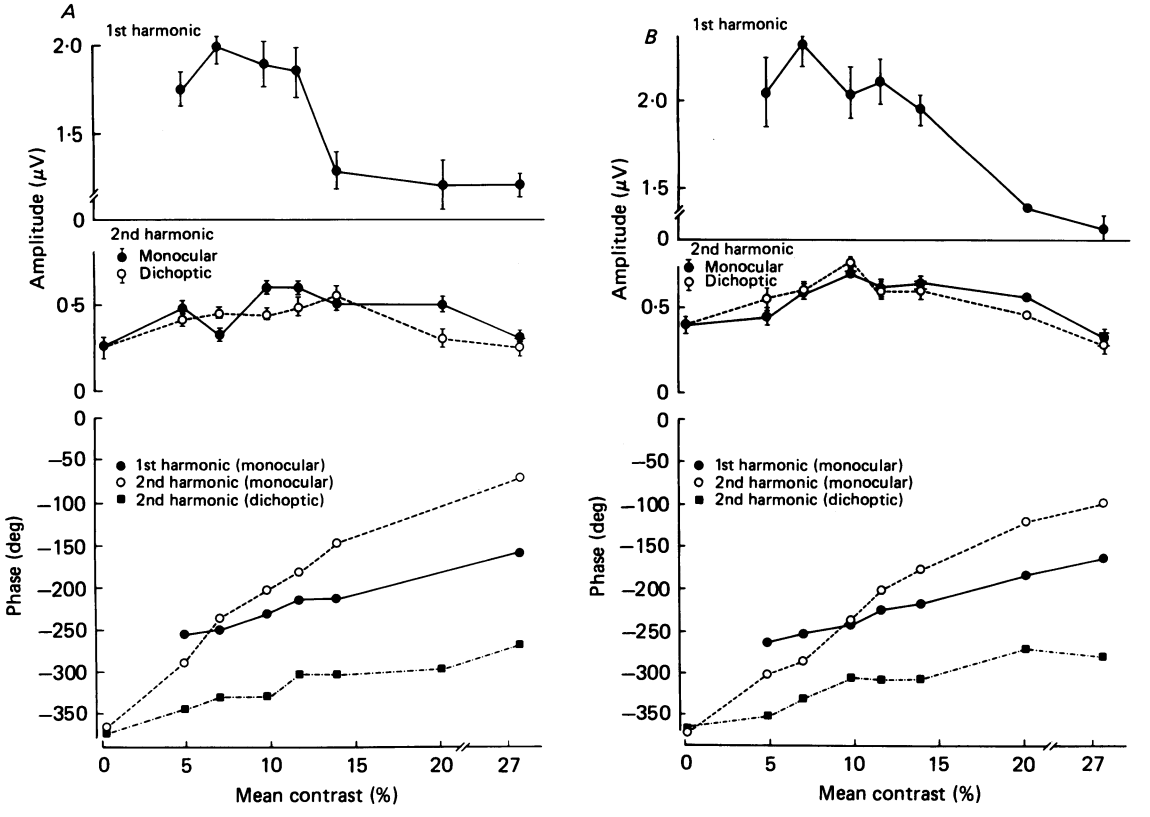

Fig. 7. Details are as for Fig. 6 except that results were obtained from observer M.M. for modulation contrasts of 6·9% (*A*) and 9·75% (*B*). Note that overmodulation occurs for mean contrasts less than ΔC.

monocular viewing. The VEP phase with dichoptic presentation is mainly determined by the absolute level of modulated contrast (ΔC), as indicated by the superposition of the phase curves for each $\bar{C}$ with each other and with that obtained for the counterphase grating.

Monocular and dichoptic response functions are compared in Figs 6 (observer P.B.) and 7 (observer M.M.) over a wider range of mean contrast levels for each ΔC. In these experiments, ΔC was held constant while mean contrast was randomly varied for each testing session (see Methods). The presented curves clearly show that, in the explored $\bar{C}$ range, peak amplitude does not occur at a modulation depth of 100% (where $\Delta C = \bar{C}$). The gain is highest between mean contrast levels of 0·08 and 0·14.

The response is therefore not simply determined by modulation depth ($\Delta C/\bar{C}$) or by absolute contrast change (ΔC). This apparent 'tuning' of amplitude with mean contrast can be explained by the relative scaling of amplitude as a function of modulation depth described earlier. These 'tuned' amplitude functions clearly show that the effect of mean contrast is not a masking effect; for a given C, there is not a monotonic decrease in amplitude with increasing levels of mean contrast but rather the response first increases and then declines. This increase occurs well above threshold and does not appear to represent contrast summation.

Again, it can be seen that for a given ΔC, the phase of the first harmonic frequency component of the monocular VEP shows little dependence on mean contrast. The phase of the second harmonic frequency component is strongly dependent on mean contrast with monocular viewing. The second harmonic frequency phase also depends, but to a lesser extent, on mean contrast with dichoptic viewing.

DISCUSSION

The present data show that both the amplitude and the phase of the steady-state VEP are determined more by the average spatial contrast of the pattern than by the absolute amount of contrast change. The controlling effect of mean spatial contrast on temporally modulated responses cannot be due to fatigue or response suppression. First, the effect of mean contrast on the VEP is not monotonic with respect to spatial contrast; response gain is highest at intermediate levels of mean contrast (Figs 6 and 7). Second, the response dependence on mean contrast is expressed differently in the fundamental and second harmonic frequency components. Third, mean contrast can produce amplification in that the absolute amplitude of the second harmonic to a contrast-modulated grating can be larger than that to only a counterphase grating of the same modulated contrast.

We have previously shown in a contrast modulation study (Bodis-Wollner *et al.* 1972) that the amplitude of the VEP elicited by contrast change is strongly affected by mean contrast. We have also shown that the VEP amplitude is not constant for a given modulation depth but increases with increasing levels of mean contrast. At first, this result seems counter-intuitive if a model of proportionality between contrast change and mean contrast ($\Delta C/\bar{C}$ = constant) is considered. The result we obtained, however, should not be surprising. It has been shown in several studies that VEP amplitude grows with stimulus contrast using 'on–off' presentation of the grating. 'On–off' presentation is the end-point (100% modulation depth) of contrast modulation such that $\Delta C = \bar{C}$ (Bodis-Wollner *et al.* 1972). Differently stated, modulation depth is equal for any 'on–off' pattern regardless of peak contrast. If the VEP amplitude function represented a form of Weber's law for contrast, then VEP amplitude should remain constant regardless of peak contrast when 'on–off' grating presentation is used. Obviously, this is not the case. It is also not the case that VEP amplitude remains constant for the same absolute contrast change (ΔC). Our study shows that a law between these two extremes (ΔC = constant *versus* $\Delta C/\bar{C}$ = constant) is operating. This law is expressed in the second harmonic frequency data as an exponential function with a similar slope across the mean contrast levels that we studied (Fig. 4). We propose that this exponential function represents contrast

gain control. Furthermore, the second harmonic frequency component of the dichoptic VEP is similarly influenced by mean contrast, suggesting a cortical source of a contrast gain control mechanism.

In the following section we shall discuss the possible contributions of pre-cortical and cortical contrast gain mechanisms to the surface-recorded VEP. Our data show that certain aspects of the contrast gain control mechanisms are expressed only in the monocular pathway. The strong phase dependence of the second harmonic frequency component on mean contrast as well as the presence of the first harmonic component occurred only with monocular contrast-modulated gratings. It is possible that the neuronal organization which determines this monocular response, although not its direct generator, is in the retina. This could be consistent with studies by Shapley & Victor (1978) which demonstrated for retinal ganglion cells that the response to contrast change can be regulated by mean contrast. It was also shown that the gain control behaviour of neurones of the lateral geniculate most likely reflects properties of retinal inputs with relatively little modification (Sclar, 1987). Thus it is not inconceivable that the VEP reflects properties of a pre-cortical contrast gain control mechanism.

The fact that the VEP is not solely determined by pre-cortical organization is revealed by the second harmonic data. We have shown that when the steady grating and the counterphase grating are presented to the same eye, the VEP contains both first and second harmonic frequency components; while, when they are presented dichoptically, the VEP only contains second harmonic frequency components. Thus, partially at least, the second harmonic component is cortically determined. The similarity between the first and second harmonic components is that the amplitudes of both are strongly dependent on the level of mean contrast and not determined by ΔC alone. They differ in three major respects: (1) the first harmonic frequency functions separate for each level of mean contrast, and therefore (2) only the second harmonic frequency data represent a unitary function of mean contrast, and (3), as stated before, the asymmetrical first harmonic frequency component of the VEP is not reflected in the dichoptic human VEP. Some of these differences between first and second harmonic functions could be interpreted in the following way. It is known that most of the surface-recorded VEP is the result of the potential difference of soma and dendrite in the depolarization of vertically oriented pyramidal-type cells (Pollen, 1969). The observed branching patterns of individual neurones (Gilbert & Wiesel, 1983) suggest that neurones other than pyramidal neurones may control the responses of vertically oriented pyramidal cells in a lateral interconnecting system. Individual neurones of the cat cortex, while differing from each other, manifest contrast gain control behaviour (Ohzawa, Sclar & Freeman, 1985). Our data show that average dichoptic contrast serves to modulate the phase and amplitude of the second harmonic frequency but does not produce a first harmonic frequency component at the surface-recorded VEP. The reason may be that dichoptic contrast adjusts the potential difference between apical dendrites and soma through synaptic contacts, but does not manifest itself as a surface-recorded response, due to the orientation of the neurones providing a lateral signal. To put this another way, the second harmonic VEP function indirectly reflects the influence of horizontally oriented cortical neurones.

Finally, it is worth considering the possible relationship of our VEP data to the division of magno- and parvocellular elements of the visual pathway. Kaplan & Shapley (1982) found that parvocellular and magnocellular neurones in the dorsal LGN are sensitive to different contrast ranges. The 'break-point' between these two populations is around 0·10 contrast. As mentioned earlier, we deliberately explored levels of mean contrast between 0·04 and 0·28 to encompass this critical range. By inspecting the gain curves in Figs 6 and 7, it is evident that these functions peak in the critical mean contrast range of 0·08–0·14. Thus, the response gain of the VEP is greatest at the point where the magnocellular and parvocellular populations intersect with respect to contrast. Evidence of the greatest VEP gain in this contrast range suggests a functional significance for the intersection of the two postulated populations. Psychophysical studies with auditory categorical perception have demonstrated that sensitivity is greater to stimuli presented near the boundary conditions of two different populations than sensitivity to two presentations arising from the same population (Repp, 1983). In this regard, our data suggest that a similar physiological category boundary may exist near the 0·10 contrast region in the human, consistent with the contrast-dependent segregation described above for magnocellular and parvocellular layers in the primate (Shapley *et al.* 1981). The possibility that contributions from both 'high' and 'low' contrast neurones may be reflected in the VEP is consistent with our earlier (Bodis-Wollner & Hendley, 1979) and with more recent psychophysical findings (Lehkey & Wilson, 1985; Gouled-Smith & Thomas, 1985). As mentioned earlier, Bodis-Wollner & Hendley (1979) have shown that psychophysical contrast modulation curves show an apparent inflexion between 0·08 and 0·14 contrasts, and this inflexion disappears using contrast adaptation. Further studies exploring response gain in human psychophysics and VEPs may be fruitful. In addition, there is a need for single-cell studies in the primate which can answer some of the questions raised by our VEP data.

In summary, we have shown that spatial contrast controls the gain of the monocular and the dichoptic human VEP. The first harmonic component is strictly monocular while the second harmonic frequency component of the VEP also reflects a cortical contrast gain control mechanism and may indirectly reflect the contribution of horizontally oriented interneurones.

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