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SUSTAINED AND TRANSIENT MECHANISMS IN THE STEADY-STATE VISUAL EVOKED POTENTIAL: ONSET PRESENTATION COMPARED TO PATTERN REVERSAL

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Summary—1. There are many reports of a region of reduced amplitude in the spatial frequency characteristics of the occipital evoked potential generated by contrast reversing sinusoidal gratings. This effect is especially common at medium spatial frequencies and therefore shows as a notch in the mean amplitude vs spatial frequency function.

2. In this report we test the idea that the region of reduced amplitude responses may be due to cancellation of signals dominated by transient and sustained mechanisms.

3. Visual evoked potentials (VEPs) elicited by 8 Hz contrast reversal are compared with those obtained using on–off stimulation at 8 and 16 Hz. Psychophysical contrast thresholds are obtained for these stimuli and the data indicate that 8 Hz contrast reversal is an effective stimulus for both transient and sustained mechanisms, whereas 16 Hz on–off is a poor stimulus for transient mechanisms.

4. The VEP data for these two conditions support this view; a principal component analysis of the VEP amplitude data shows that two statistically independent sources contribute to the 8 Hz contrast-reversal response and that the 16 Hz on–off response is derived from a single source.

5. The obtained factors exhibit spatial tuning as described for sustained and transient mechanisms. As reported previously, it is shown that for many, but not all subjects, the 8 Hz contrast-reversing stimulus leads to a pronounced notch in the mean amplitude vs spatial frequency response function indicative of the suspected interaction of sustained and transient channels.

6. In general, the 16 Hz on–off response does not show the notch, reflecting the activity of a single channel. It is of practical interest that the 16 Hz on–off VEP data exhibit high interindividual reliability and that their spatial tuning characteristics match those of the contrast sensitivity function. These properties suggest that for objective measurement of psychophysical thresholds on–off stimulation at 16 Hz is likely to yield more reliable data than contrast reversal.

Key words—Visual evoked potential; transient/sustained theory; steady state; on–off; pattern reversal.

INTRODUCTION

The relationship between visual evoked potentials (VEPs) and stimulus visibility remains obscure. Many authors have established that VEPs can be used to predict contrast thresholds (e.g. Campbell and Maffei, 1970; Kulikowski, 1977a; Cannon, 1983) but above threshold there are conditions under which the VEP behaves as if it is entirely unrelated to perception. For example, when VEP amplitude vs spatial frequency is plotted, for many subjects there are ranges of spatial frequency where the response is close to noise level. Such unexpected low amplitude responses may occur at all spatial frequencies but are especially often present at 2–4 c/deg. As a result, a bimodal function is obtained in the mean over subjects, and also in some subjects' individual responses, with VEP amplitude being markedly attenuated around 2–4 c/deg (Tyler *et al.*, 1978; Tyler and Apkarian, 1985; Strasburger *et al.*, 1986, 1988; Bach and Joost, 1989; Joost and Bach, 1990). This so-called spatial frequency "notch" is particularly surprising because it occurs in the range of spatial frequencies at which observers have maximum contrast sensitivity.

This paradox of obtaining a small signal from a highly visible stimulus occurs under a variety of conditions, depends on electrode position, presentation rate, and which signal components are extracted. There is little doubt, however, that it limits the applicability of VEPs (for reviews see Strasburger *et al.*, 1988; Bach and Joost, 1989). A possible explanation for this effect is that more than one neuronal subsystem is being stimulated and that the notch represents the effects of signal cancellation taking place at spatial frequencies where these subsystems overlap. In the present report we consider the possibility that the subsystems in question are the sustained and transient mechanisms as described by Kulikowski and Tolhurst (1973). These authors used on–off and contrast-reversal stimulation in a threshold-based psychophysical paradigm. If the VEP spatial frequency notch can be explained in these terms then specific predictions follow about the differences between VEP responses generated by contrast reversal and those generated by on–off presentation. We have therefore compared VEPs obtained with the two forms of stimulation for a wide range of spatial frequencies and contrasts.

To generate VEPs, stimuli must be temporally modulated and in order to obtain a direct comparison to detectability the psychophysical observations must be based on temporally modulated rather than static gratings. The finding made by Kulikowski and Tolhurst (1973) is that there are two thresholds evident when gratings are temporally modulated: one for the detection of movement and the other for the detection of the spatial structure. The fact that these two thresholds vary independently with temporal and spatial frequency suggested that they represent the limits of two separate processing channels, one optimized for the detection of temporal change and the other optimized for the detection of spatial change. The two channels were referred to as movement and pattern systems, respectively (Kulikowski and Tolhurst, 1973). The channels detecting movement favour low spatial frequency whilst those discriminating spatial structure favour high spatial frequencies.

Psychophysical and perceptual observations on the transition region between these two systems can serve as a basis for the interpretation of the rapid presentation VEP data described here. There is a qualitative change in the appearance of a contrast reversing grating when spatial frequency is increased from 1 to 4 c/deg; at the lower spatial frequency apparent movement dominates the perception of the grating, but at 4 c/deg and above the pattern is more easily recognized and the impression of movement is much less compelling. Kulikowski and Tolhurst (1973) showed that detection processes change in parallel with these perceptual observations. At low spatial frequencies observers were twice as sensitive to the contrast-reversing stimulus as they were to the on–off stimulus. Since the physical contrast change for reversal is twice that for on–off, this was regarded as evidence that the low-spatial-frequency mechanism is mediated by transient-like detectors and relies on the change in contrast between two consecutive phases of the stimulation rather than on the maximum contrast. At higher spatial frequencies the contrast-change rule does not apply; as spatial frequency is increased from 1 to 6 c/deg there is a gradual transition in the relative sensitivity to reversal and on–off stimuli, so that at 6 c/deg they are equally detectable. At still greater spatial frequencies the detecting mechanism relies on standing contrast.

The range of 1–4 c/deg where this transition between pattern and movement processing takes place is also the range where the notch in the mean VEP amplitude function is found; this raises the possibility that the notch may be a manifestation of sustained/transient interaction. The first step in determining if this is the case is to compare, *in the same subjects*, VEP responses to stimulus conditions which differ in their relative effectiveness of stimulating these subsystems.

METHODS

The following is a brief account of the methods used in the present study. They have been more fully described in previous papers (Strasburger and Rentschler, 1986; Strasburger, 1987; Strasburger *et al.*, 1988).

Stimulus patterns and procedure

An LSI-11/23 computer generated the stimuli, recorded the EEG, and performed the data analysis off-line. Temporally modulated vertically oriented sine-wave gratings of variable spatial frequency and contrast were presented on a HP-1310A display with a mean luminance of 17 cd/m^2. The display was calibrated for a linear luminance characteristic up to 95% contrast. The frame rate was 64 Hz.

The stimuli were grouped into sets of up to eighteen; a sampled sweep was realized by presenting the stimuli of a set one after the other for 3 s each, alternating the ascending/descending order several times. No EEG was recorded during the first second of each stimulus to allow the VEP to attain a steady state. Net presentation time was at least 12 s for each stimulus. Stimuli of a set differed in spatial frequency or in contrast, depending on which sweep was chosen. Subjects viewed the screen binocularly from a distance of 128 cm, whereby the circular test field subtended 5 deg of arc. A fixation point was positioned in the centre of the field.

Two kinds of temporal modulation were employed: pattern reversal and on–off. The stimulus intensity in both cases is

$$I(x,t) = I_{\text{mean}}(1 + C(t)\sin\omega_x x) \quad (1)$$

where x is the horizontal spatial coordinate (deg); t is time (s); I_{mean} is space average luminance (cd/m^2); $\omega_x = 2\pi f_x$; and f_x is spatial frequency (c/deg).

$C(t)$ is the temporal modulation function given, for pattern reversal and on–off, respectively, by

$$C_{\text{rev}}(t) = C_{\text{m}}\sin\omega_t t \quad \text{and}$$

$$C_{\text{oo}}(t) = \tfrac{1}{2}C_{\text{m}}(1 + \sin\omega_t t) \quad (2)$$

where C_{m} is maximum contrast $= (I_{\text{max}} - I_{\text{min}})/(I_{\text{max}} + I_{\text{min}})$; $\omega_t = 2\pi f_t$; f_t is temporal modulation frequency (Hz).

The absolute value of $C(t)$ is the pattern contrast at any given moment in time. For pattern reversal a modulation frequency f_t of 8 Hz (i.e. 16 rev/s) was used because this is a commonly used stimulus and allows us to compare our results with those of other workers. On–off stimulation was at 8 and 16 Hz. Note that modulation rates of reversal and on–off cannot be directly compared, as is discussed in the Appendix.

Recording

A bipolar electrode montage was used with one electrode placed midline 2 cm above the inion and the other on the forehead, two-thirds of the distance from inion to nasion. Grass gold cup electrodes with a shielded differential cable were used. The shield was connected to one ear. Electrode impedance was kept below 2 kΩ.

Data analysis

The EEG was band-pass filtered (1 and 25 Hz, 12 dB) and sampled at a rate of 64 Hz.* In the following off-line extraction of the VEP by means of averaging and spectral analysis, only the multiples of the stimulation frequency were considered. These were the components at 8 and 16 Hz. The 24 Hz component was neglected for its low signal-to-noise ratio; higher frequency components did not occur due to the limitation imposed by the sampling rate. For reversal stimulation, only the second harmonic (i.e. 16 Hz) is reported. The first harmonic, as others have noted, shows no relationship to the stimulus. For 8 Hz on–off modulation, both first and second harmonics were extracted. Only the second harmonic results are reported, however, since the first harmonic showed excessive *intra*-subject variability. With 16 Hz on–off stimulation, only the first harmonic was obtained.

Continuous plots of temporal phase were obtained by using a principle of minimum phase difference (Strasburger, 1987). That is, appropriate multiples of 360 deg were added such that phase values of adjacent points had minimum distance. Sampling along the spatial frequency axis was fine enough for this procedure to yield unambiguous phase results in most cases. In the region of the notch, however, phase is less reliable and usually shows large variation with varying spatial frequency, so that additional constraints are required in order to resolve the cyclic ambiguity there. One solution is to obtain data with both spatial frequency and contrast as independent variables; in these cases minimum variation across both variables was sought. In the few remaining ambiguous data points, we have preferred to show phase as increasing with increasing spatial frequency since increasing phase is found for most of our data, so that increasing phase at the ambiguous data point results in a smooth trajectory (i.e. a continuous first derivative), and there is also wide agreement in the literature about a general phase increase with increasing spatial frequency (see review in Strasburger *et al.*, 1988, p. 1085).

Subjects

Twenty emmetropes between 19 and 28 yr, one aged 39, served as paid subjects. The number of males and females was equal.

*A sampling rate of 64 Hz might seem unduly low. Its use precludes, for example, the analysis of the second harmonic of the 16 Hz on–off response and also precludes the use of a 16 Hz pattern–reversal stimulation. The sampling rate was chosen in order to be able to phase-lock the sampling rate to the display frame rate. A higher frame rate, e.g. 128 Hz, was not desirable since it would have reduced stimulus luminance. A solution would have been to use two sample points per frame but this was not possible with our setup. On the other hand, we find the common practice of using free-running display refresh, unlocked to the sampling process, unsatisfactory. Non-linear modulation might give rise to cross-modulation between frame refresh and the EEG sampling process, and artifacts are to be expected at the difference frequency. When this difference frequency is not known, as is the case with a free running frame refresh, it is hard to isolate artifacts resulting from this origin.

Contrast sensitivity function

Thresholds for detecting movement or temporal change differ—especially at low spatial frequencies—from thresholds for the detection of pattern striation (Kulikowski and Tolhurst, 1973; Hilz *et al.*, 1981). Reliable determination of pattern and movement thresholds requires considerable experience, however. We have chosen to avoid the complexities associated with pattern and movement criteria and used a pure detection criterion. Subjects were asked to set absolute contrast threshold using a hand-held potentiometer for the adjustment. The average of at least three settings was taken. Stimuli were presented at the same set-up that served for the VEP recording and the same forms of temporal modulation were used.

RESULTS

The data in Fig. 1 illustrate the major influence which the mode of presentation has on VEP amplitude vs spatial frequency functions. Twenty subjects were included in this study. For the purpose of presentation, the subjects are sorted such that figure parts a and b show the subjects with more pronounced response attenuation in the reversal response so as to make it easier to see whether this effect would be evident in the on–off function. Three stimulus conditions, reversal 8 Hz, on–off 8 Hz and on-off 16 Hz are compared. Contrast is 40%. The left column in Fig. 1 shows the responses for the contrast-reversal stimulation; amplitude and phase of the 16 Hz (i.e. second harmonic) component are plotted as a function of spatial frequency. The results confirm previous reports. The shape of the function varies considerably between subjects but some general characteristics are apparent. In some subjects (AR, FS, IH, and RV) the attenuated response is confined to a narrow range of spatial frequencies and can be referred to as a notch. In the other cases the loss of amplitude occurs for a range of spatial frequencies. The temporal phase of the contrast reversal data generally increases with spatial frequency and in many cases (AR, DS, FS, GS, IH, KC, MB, RT) undergoes a large phase shift which coincides with the notch.

The centre column in Fig. 1 illustrates the form of the amplitude/spatial frequency functions for the 16 Hz (i.e. second harmonic) component when the on–off 8 Hz stimulation is used. The data appear even more variable than for pattern reversal. In some cases the amplitude plots have a region of low amplitude which seems loosely related to the appearance of a notch in the reversal data. The phase data do not reflect this variability, however. Phase is largely independent of spatial frequency, except for one subject (FS) who shows a pronounced monotonic increase with increasing spatial frequency.

These second harmonic amplitude data, though highly variable between subjects, were at least highly repeatable within any one subject. In contrast, the strong first harmonic component, which we found for 8 Hz on–off stimulation, had excessive *intra*-subject variability. A relationship of this component to stimulus conditions could thus not be established. We consider the 8 Hz activity as disturbed by noise and have not shown the data. Note that an explanation based on a shift of signal energy between first and second harmonic cannot account for the first-harmonic intra-subject variability, since the second harmonic was reliable.

The third condition tested, on–off modulation at 16 Hz, was chosen because it has the same appearance/disappearance rate as the 8 Hz pattern-reversal stimulus. This stimulus leads to a quite different response pattern (Fig. 1, right column). Unlike the reversal data there is no middle range of spatial frequencies where loss of signal occurs and overall the shape of the response function is similar to that of the normal contrast sensitivity curve. The correspondence with the psychophysics is accompanied by a relatively constant phase response. Phase is mostly constant with increasing spatial frequency with an occasional slight increase at high spatial frequencies. Phase responses both within and between subjects are repeatable.

To shed light on the structure of the data variability, we have performed a principal component analysis (PCA) on the amplitude data from the two conditions with most dissimilar results shown in Fig. 1, 8 Hz reversal and 16 Hz on–off (left and right columns). The 18 spatial frequencies were treated as variables. The PCA yielded four factors with eigenvalues >1.0 (Table 1) of which the two largest factors are considered in the following. These two factors accounted for 60–70% of the total variance.

The pattern of distribution of variance among the factors turns out to be quite different between 8 Hz pattern reversal and 16 Hz on–off. Whereas the large majority of on–off variance (61%) is explained by only a single factor, the

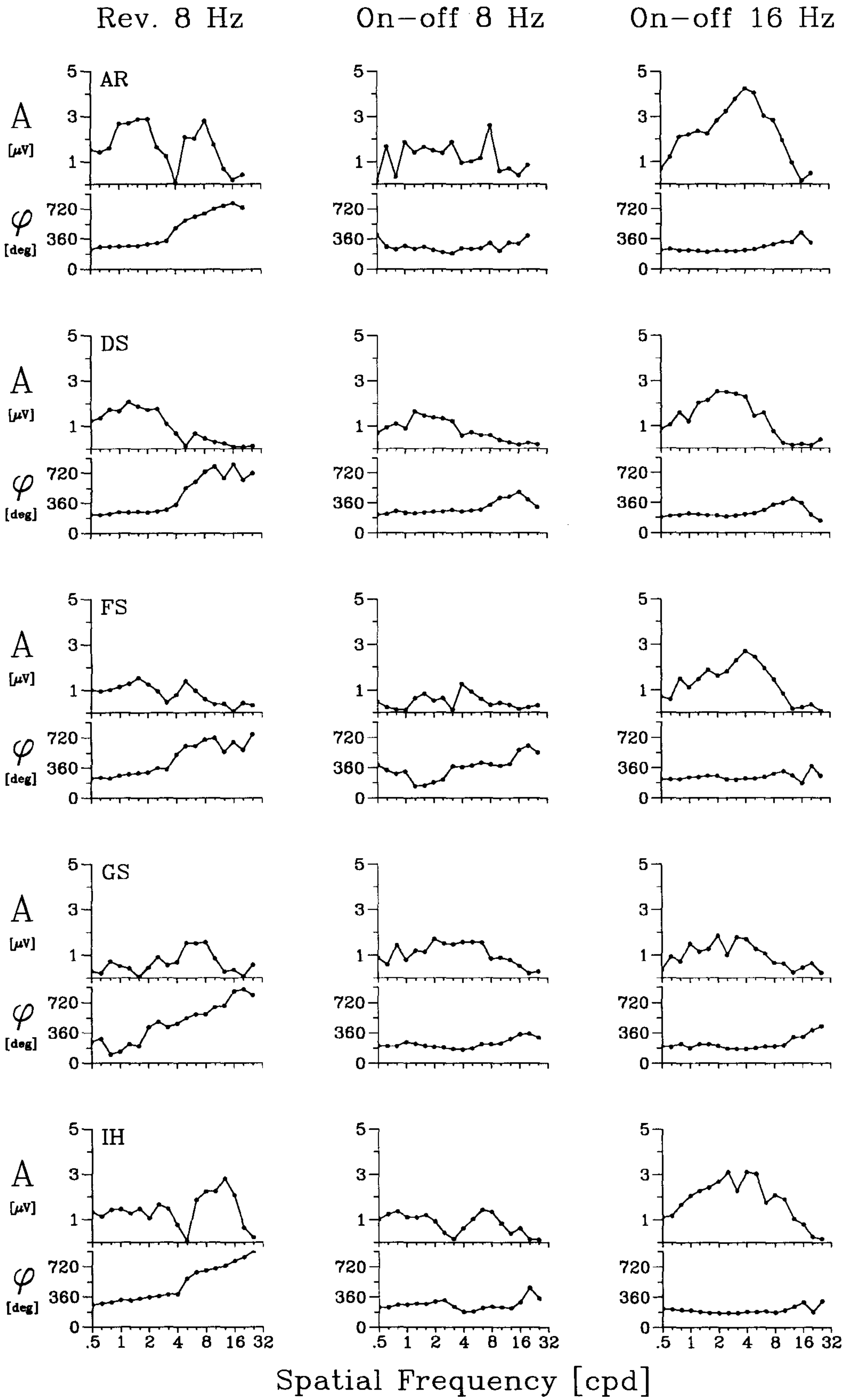

Fig. 1(a). *Caption on p. 219.*

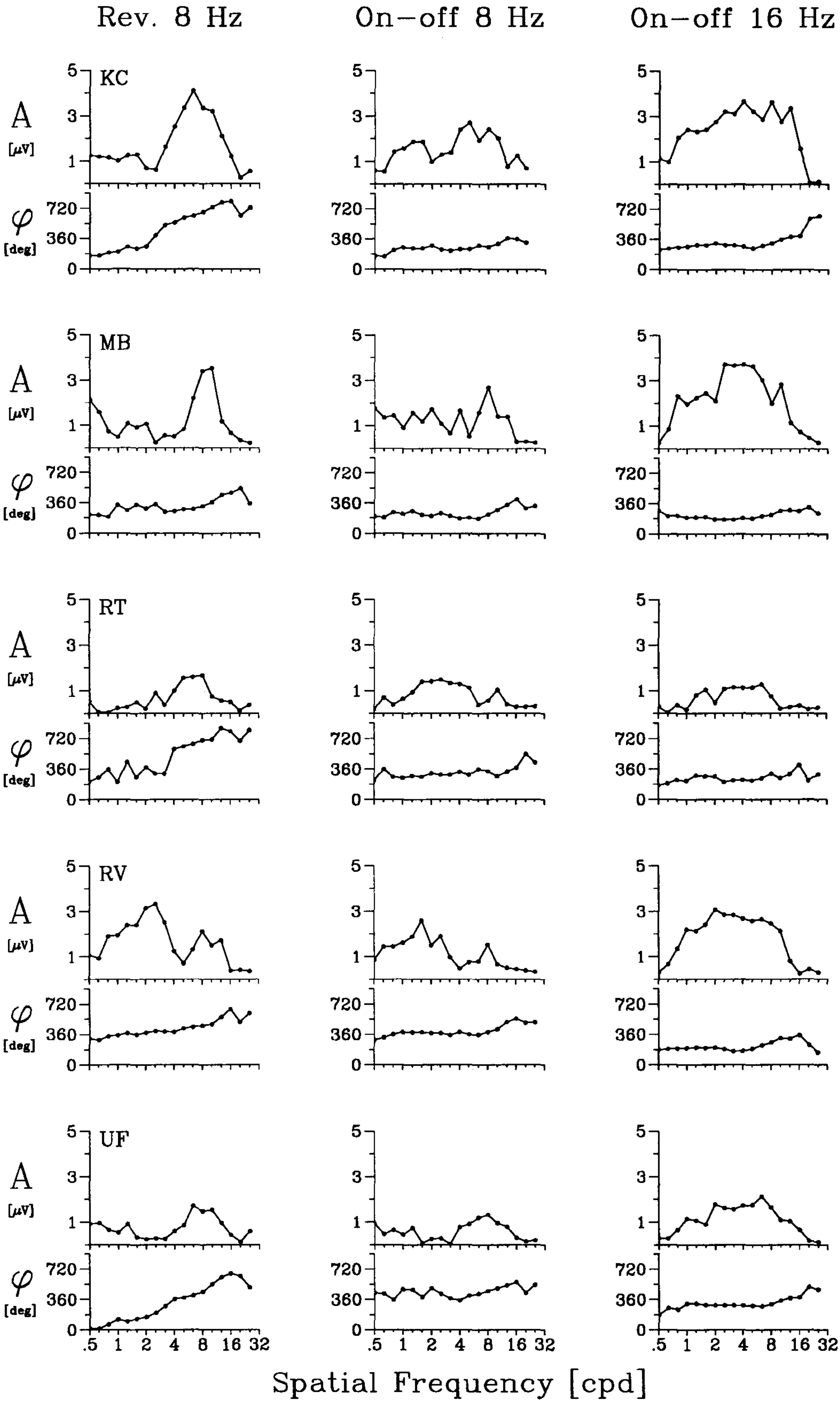

Fig. 1(b). *Caption on p. 219.*

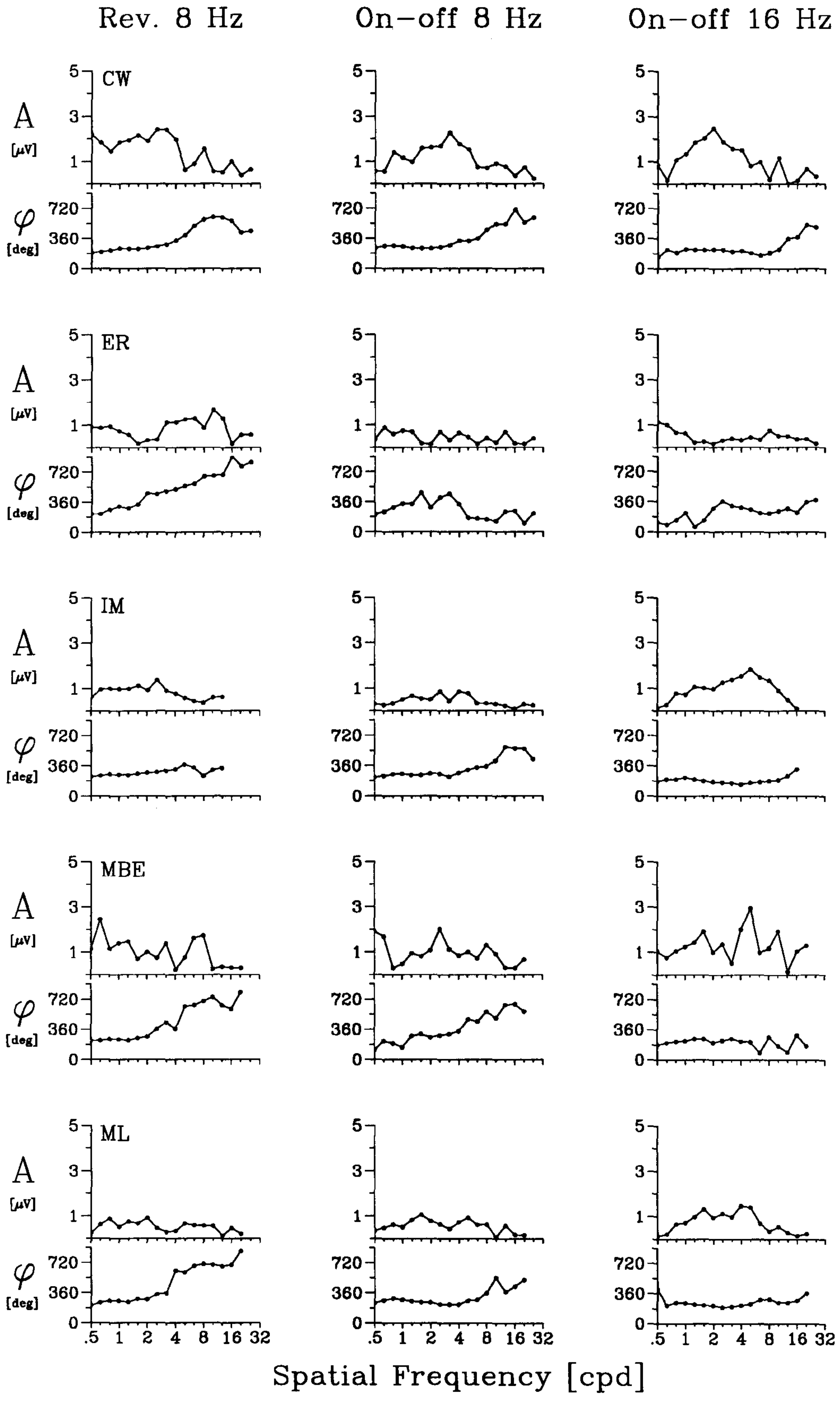

Fig. 1(c). *Caption on p. 219.*

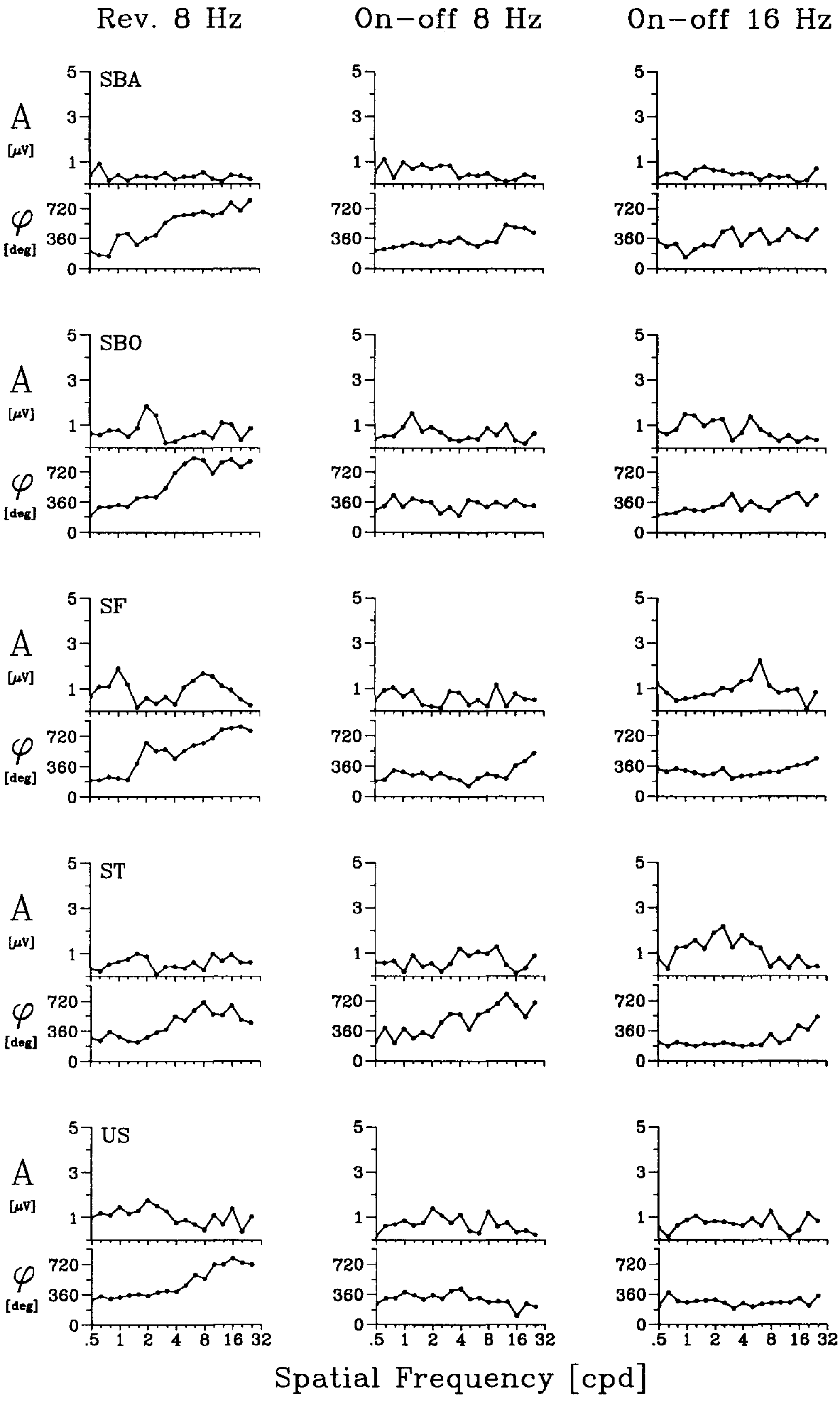

Fig. (1d). *Caption on facing page.*

Table 1. Principal component analysis of amplitude data from Fig. 1: variance explained by factors having eigenvalues >1.0

	Pattern reversal 8 Hz	On–off 16 Hz
Factor 1	39.0	61.2
Factor 2	23.0	12.2
Factor 3	10.6	7.1
Factor 4	8.7	6.0
Factor 1 + 2	62.0	73.4

variance in the pattern-reversal data is distributed more evenly, in approximately a 3:2 ratio between the first two factors. The 16 Hz on–off data thus constitute a homogeneous set with amplitude variation between subjects essentially stemming from a single source of variance, whereas two sources of variance contribute in the pattern-reversal case.

To identify these two sources of variance in pattern-reversal, i.e. to obtain physically interpretable factors, the factor solution was rotated according to the varimax criterion. Figure 2 shows the resulting factor loadings. A simple pattern is obtained. One factor, accounting for 39% of the variance, represents low spatial frequencies, from 0.5 c/deg up to 3.2 c/deg; the other factor, accounting for 20% variance, represents high spatial frequencies, from 4 up to 25 c/deg, together with some loadings on the lowest spatial frequencies. Medium spatial frequencies, in a narrow range (2.8–3.6 c/deg), are shared among the two factors.

Figure 3 shows the grand averages over subjects for these two conditions, 8 Hz pattern reversal [Fig. 3(a, b)], and 16 Hz on–off [Fig. 3(c)]. The notch at medium spatial frequency, often seen in the individual data, is still present although reduced since it occurs at slightly different spatial frequencies. Figure 3(b) serves to illustrate the variability underlying the pattern-reversal response function. Subjects have been divided into two subgroups, according to whether they scored higher on factor 1, or on factor 2, and the mean response for the two groups is shown. Subjects of type 1 have high amplitude at spatial frequencies below the notch, and subjects of type 2 have high amplitude on spatial frequencies above the notch. Both have low response in a narrow medium range. Figure 3(c) shows the 16 Hz on–off response which, after normalising the amplitudes and averaging across subjects as shown, resembles a normal contrast sensitivity function, having a conspicuous low spatial frequency cut. In summary, it emerges that the amplitude vs spatial frequency function obtained with 16 Hz on–off stimulation has a surprising similarity to the normal contrast sensitivity function which is not the case for contrast reversal stimulation.

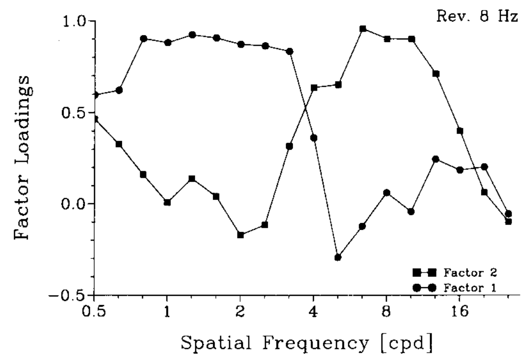

Fig. 2. Factor loadings on the two main factors obtained in a principal component analysis of the 8 Hz pattern-reversal amplitude data of Fig. 1. Factors were rotated according to the varimax criterion. Factor 1 (circles), which accounts for 39% of the total amplitude variance, mainly correlates with low spatial frequencies up to 3 c/deg; factor 2 (squares), which accounts for 23% of the variance, correlates with spatial frequencies above 3 c/deg, and also has some loadings on the lowest spatial frequencies.

The effects of contrast

The data illustrated in Figs 1–3 were recorded using contrast of 40%. The influence of stimulus contrast is addressed in Fig. 4 which is a series of three-dimensional plots of amplitude vs contrast and spatial frequency and phase vs contrast and spatial frequency. Data from three subjects were collected but for brevity only two are shown here. The third subject (RV) shows a similar amplitude response but different phase characteristics. These are not discussed here.

Fig. 1. Steady-state VEP response to temporally modulated vertical sine-wave gratings of 40% contrast. Three modes of modulation are compared: sinusoidal pattern reversal at 8 Hz, i.e. 16 reversals/s (left column), and sinusoidal appearance–disappearance at a rate of 8 (middle) and 16 Hz (right). For each of the 20 subjects amplitude and phase of the 16 Hz component are shown vs grating spatial frequency. Subjects are sorted such that (a) and (b) show those subjects with a more pronounced response attenuation at pattern reversal stimulation. (At five data points in p/r data, subjects DS, FS, GS, MB, and RT, phase in the region of the notch has not been plotted according to the principle of minimum phase difference but as increasing by more than 180 deg, cf. Methods.)

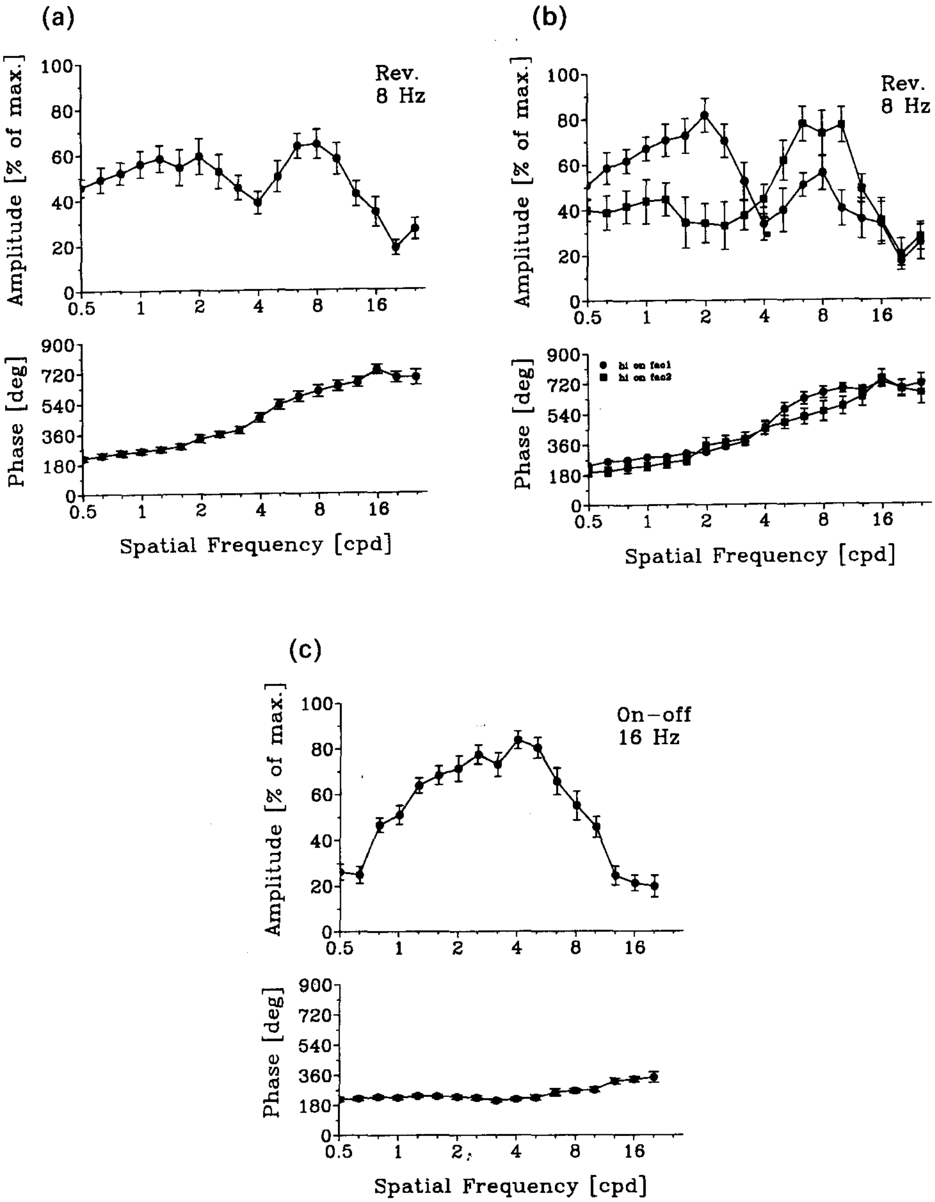

Fig. 3. Mean normalized VEP response for 8 Hz pattern reversal (a, b) and 16 Hz on–off (c), averaged over the subjects shown in Fig. 1. In (b) subjects have been divided into two subgroups, on the basis of their factor scores in the principal component analysis. Subjects AR, CW, DS, FS, IH, MBE, ML, RV, SBO, and US scored higher on factor 1; and subjects GS, IM, KC, MB, RT, SBA, SF, ST, and UF scored higher on factor 2. Subject SBA and, for on–off, subject ER have been left out of the averaging since they showed very low amplitude. Vertical bars denote standard error of the mean.

Fig. 4. (*facing page*) Pattern reversal 8 Hz, i.e. 16 reversals/s, (left) and on–off 16 Hz (right) modulation compared for a range of spatial frequencies and contrasts (between 5 and 80%), for two subjects. The phase plots are rotated relative to the amplitude plots by 180 deg in order to avoid high phase values concealing low values. Note that the phase axis for subject KC, reversal, starts from 0 deg rather than 180 deg. The on–off phase values in the rear left corner are probably due to noise.

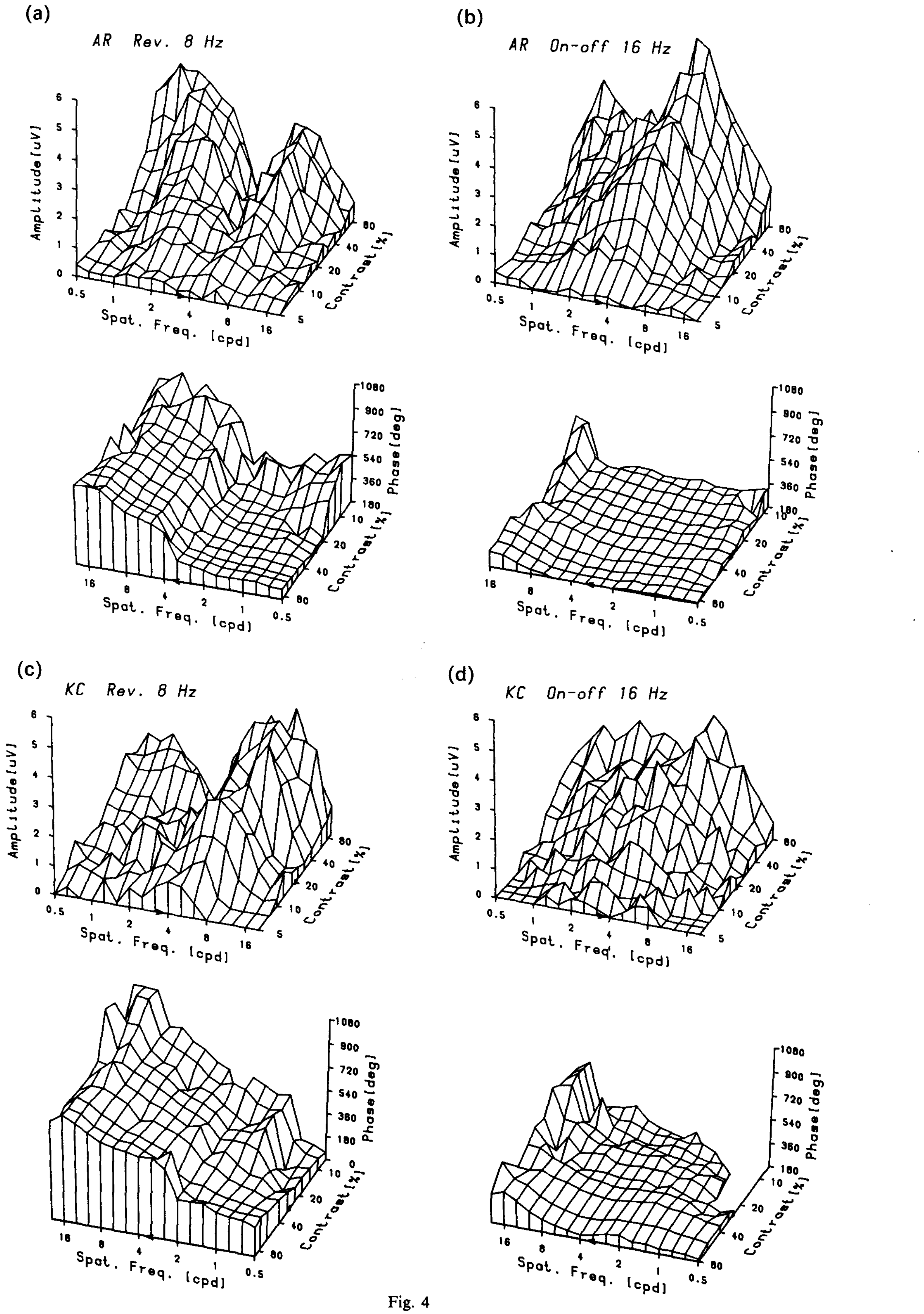
(a)
AR Rev. 8 Hz
Amplitude [uV]
Spat. Freq. [cpd]
Contrast [%]
Phase [deg]
(b)
AR On-off 16 Hz
Amplitude [uV]
Spat. Freq. [cpd]
Contrast [%]
Phase [deg]
(c)
KC Rev. 8 Hz
Amplitude [uV]
Spat. Freq. [cpd]
Contrast [%]
Phase [deg]
(d)
KC On-off 16 Hz
Amplitude [uV]
Spat. Freq. [cpd]
Contrast [%]
Phase [deg]

Fig. 4

Again the results for the contrast reversing stimulus confirm previous findings (Tyler and Apkarian, 1985; Strasburger *et al.*, 1986, 1988). Figure 4(a) (subject AR) shows that the depth of the notch appears enhanced by increasing contrast. The notch is first present at a contrast of 10%. As contrast is increased the response generated by spatial frequencies either side of the notch increases but the signal obtained from the 4 c/deg stimulus is independent of contrast. The phase data exhibit the characteristic phase shift at the spatial frequency (4 c/deg) where the notch occurs (note that the phase plot axes are rotated by 180 deg relative to the amplitude plots). The amplitude data in Fig. 4(c) (subject KC) is similar to Fig. 4(a) in that the attenuated response is more apparent at higher contrast. In this subject, however, a signal is recordable at the lower range of contrasts where the notch is not present.

When on–off 16 Hz is used the overall shape of the function remains unchanged for a wide range of contrasts. In Fig. 4(b) (subject AR) and Fig. 4(d) (subject KC) the attenuated signal is apparent at high contrast, above about 55% for both subjects.

The phase results show that the characteristics observed at 40% generalize to a wide range of contrast. Pattern-reversal phase, as has been reported by others, shows a large increase (around two revolutions) with spatial frequency; for subject AR the increase is more pronounced in the region of the notch. Furthermore, phase increases with decreasing contrast as has often been noted. Both these characteristics are absent in the 16 Hz on–off condition; phase is strikingly independent of both spatial frequency and contrast in this case.

The amplitude vs contrast function within the notch

In order to emphasize the different behaviour of 8 Hz pattern reversal and 16 Hz on–off, Fig. 5 shows the amplitude/contrast relationship for the two subjects in Fig. 4 for three spatial frequencies. Spatial frequency is chosen to be either below, above, or in the region where the reduced amplitude response, or notch, occurs. Arrows indicate contrast thresholds for the corresponding conditions (pr = pattern reversal, oo = on–off) obtained on the same apparatus. Solid symbols depict contrast reversal and empty symbols on–off stimulation. When contrast reversal is used the amplitude response obtained from spatial frequencies within the notch appears independent of contrast so that an extrapolated threshold cannot be determined. For some ranges of contrast, amplitude may decrease as contrast increases. This effect does not occur when on–off stimulation is used because, apart from high contrasts, the notch is absent. At spatial frequencies above and below the notch both onset and contrast reversal presentation permit reliable extrapolation of threshold. For both stimuli there is an over-estimation of psychophysical thresholds. Possible reasons for this are discussed below.

VEP thresholds

The higher reliability and smoothness of the 16 Hz on–of response [Fig. 3(c)] leads one to expect that the threshold extrapolation method would work well with it. That this is indeed the case is shown in Fig. 6. A full range of sensitivities derived from extrapolated thresholds, both for reversal (left) and on–off (right) stimulation, is shown together with psychophysical contrast sensitivity obtained on the same subject under the same conditions. The analysis was performed on three subjects (AR, KC, RV); the data illustrated (subject RV) are representative of the results. The procedure is applied straight forwardly for the 16 Hz on–off data but is somewhat ambiguous for the reversal data in the region of the notch. In the extrapolation procedure there are cases when a single straight line function does not fit the amplitude vs log contrast plot. In these cases two linear regression lines have been used, one for low contrast (LC) and another, steeper line, for higher contrast (HC). Both extrapolated thresholds are then shown. As is apparent from the figure, thresholds are consistently 0.7–1.0 log units below subjective sensitivities (see Discussion). The mean difference between psychophysical and VEP thresholds for this subject is 0.73 ± 0.13 for reversal, 0.82 ± 0.15 for on–off/high contrast branch, and 0.78 ± 0.10 for on–off/low contrast branch. The threshold difference for the shown subject tends to increase towards low spatial frequencies; for the reversal data the difference is 0.57 log units at 25 c/deg and increases by 0.32 log units to 0.89 at 0.5 c/deg (obtained by linear regression). This tendency is more pronounced for the reversal data of the other two subjects. Subject AR's increase is 0.91 log units (from 0.23 log units at 25 c/deg to 1.14 log units at 0.5 c/deg); for KC the increase is 0.69 log units (from 0.37 at 25 c/deg to 1.06 at 0.5 c/deg, again by

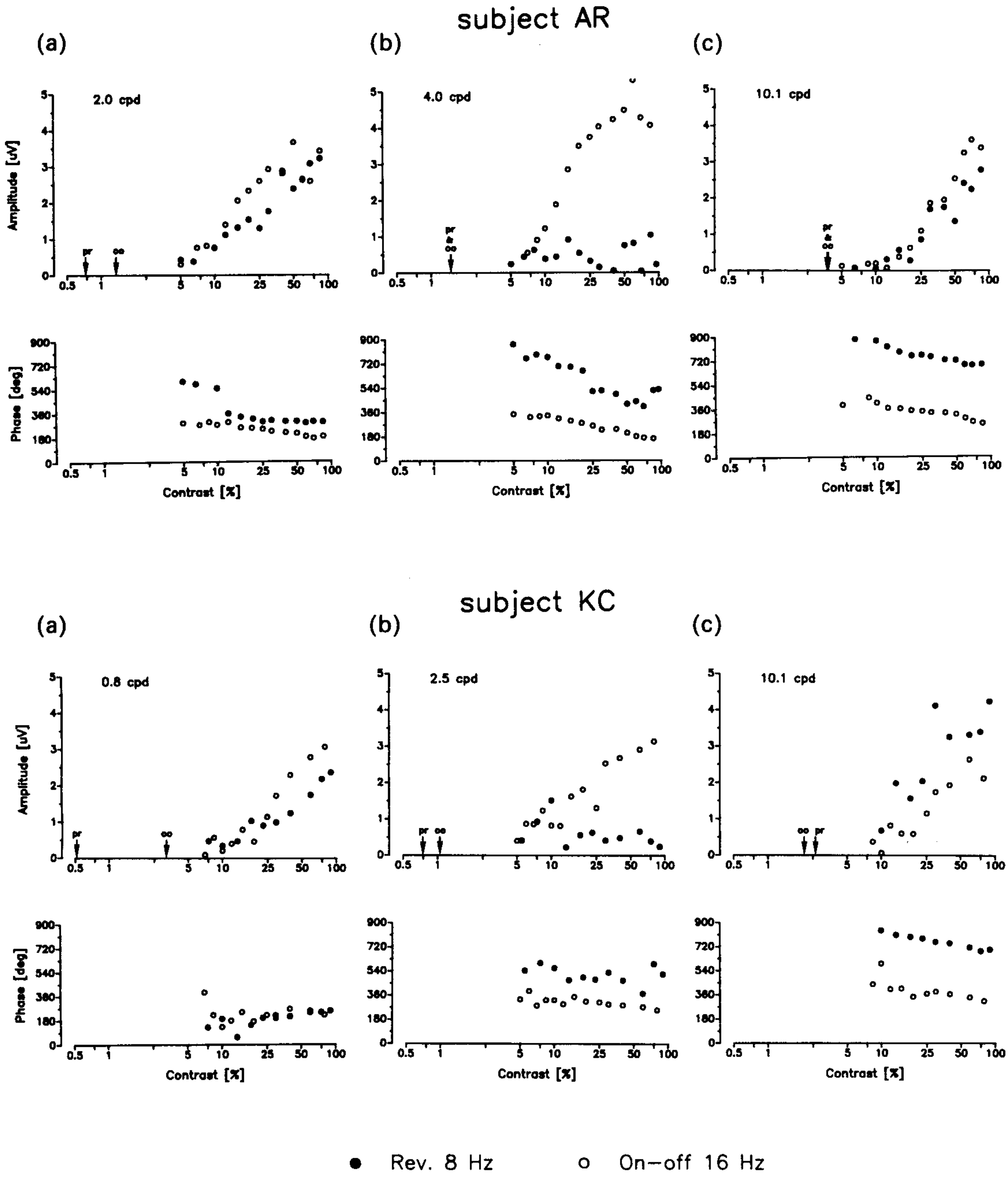

Fig. 5. Data from Fig. 4, replotted as a function of contrast. Three spatial frequencies have been chosen for each subject: below the notch (a), in the notch (b), and above the notch (c). Solid circles, pattern reversal; open circles, on–off. Note that the phase difference of >360 deg between on–off and reversal is a consequence of Fig. 4 in which the principle of minimum phase difference was applied along the spatial frequency axis. The arrows show subjective contrast thresholds, determined with a pure detection criterion by the method of adjustment on the same setup. Reversal threshold, pr; on–off threshold, oo.

linear regression). Such a divergence of the curves is only slight or absent in the on–off data. Consequently, the shape of the on–off VEP threshold curves is more similar to the subjective curves than is the case for reversal stimulation. Interestingly, when the curve shape is considered (i.e. assuming a constant offset), the better predictions for reversal stimulation were obtained with low-contrast extrapolation (LC) whereas for on–off the predictions were better with high-contrast extrapolation (HC). This was most evident for subject AR. Note that the

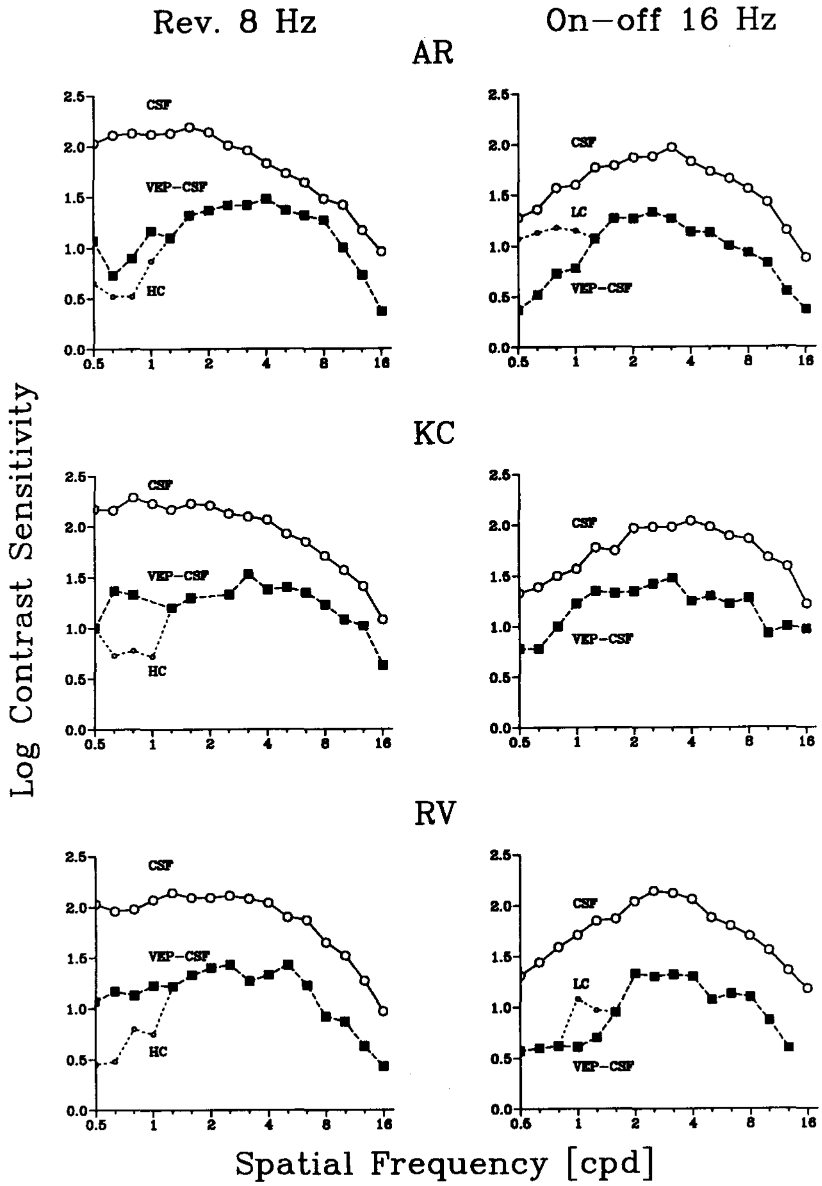

Fig. 6. Contrast sensitivity derived from VEP extrapolations compared to subjective contrast sensitivity obtained from the same subject under identical stimulation conditions. Reversal stimulation (left), on–off 16 Hz stimulation (right). Extrapolations from low and high contrast ranges, where different, are denoted by LC and HC.

major differences between the high and low contrast regressions are at low spatial frequencies.

Psychophysical thresholds

To obtain a basis for the interpretation of our VEP results, psychophysical contrast sensitivity functions have been gathered for the three different stimulus conditions used to generate VEPs. The results are shown in Fig. 7 (8 Hz reversal, open circles; 8 Hz on–off, open squares; 16 Hz, on–off solid squares) together with static contrast sensitivity (solid circles). Absolute detection thresholds rather than movement or flicker thresholds have been determined, i.e. the subjects were instructed to report when they could detect the presence of the stimulus when compared to a blank screen. The influence of the mode of presentation is particularly evident at low (< 3 c/deg) spatial frequencies. The means of five subjects are presented (AR, FS, KC, RV, UF). Maximum sensitivity at low spatial frequencies is obtained with 8 Hz contrast reversal. As reported previously (Kulikowski, 1971; Kulikowski and Tolhurst, 1973) sensitivity to the 8 Hz on–off stimulation is only half that for contrast reversal at spatial frequencies below 3 c/deg. The fact that there is a strong low spatial frequency cut in the 16 Hz on–off data indicates that transient mechanisms (which are particularly sensitive at low spatial frequencies) are not being strongly activated (see Discussion). The shape of the 16 Hz on–off curve is very similar to the static curve. Indeed, above 1.6 c/deg, the difference is a constant 0.22 log units (only 0.03 log units standard deviation). 16 Hz on–off contrast sensitivity is thus fully determined by sustained mechanisms above 1.6 c/deg. Below 1.6 c/deg the offset becomes slightly smaller (decreasing to 0.09 log units) indicating an additional slight transient activation. The offset shows that maximum contrast [see Appendix, equation (3)] is not the relevant parameter for on–off. The effective contrast is 60% (corresponding to −0.22 log units) of maximum contrast, i.e. a little more than that of the static stimulus component.

The same is true for the 8 Hz on–off response above a spatial frequency of 2 c/deg, where 8 and 16 Hz on–off lead to nearly identical sensitivity. Below 1 c/deg, strong transient responses are elicited by 8 Hz on–off.

Surprisingly, although on–off stimulation has been well studied (cf. e.g. Kulikowski *et al.*'s work in the early seventies), the described similarity of contrast sensitivity between *fast* on–off and static presentation has not been reported before. Perceptually, fast on–off modulated gratings appear very similar to static gratings.

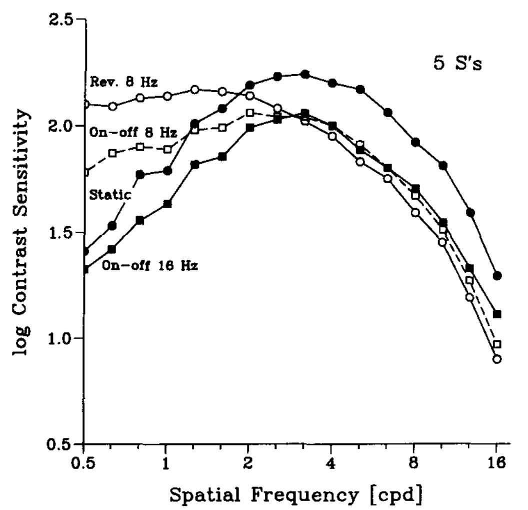

Fig. 7. Mean contrast sensitivity for four modes of temporal modulation: pattern reversal at 8 Hz (i.e. 16 reversals/s) (open circles), on–off 8 Hz (open squares), on–off 16 Hz (solid squares), and static gratings (solid circles). Mean of five subjects.

DISCUSSION

The two-peaked spatial frequency function and transient and sustained mechanisms

The main issue addressed in this paper is the influence of the mode of stimulus presentation on the spatial characteristics of the steady-state VEP. Previous authors have described a two-peaked function (or notch) when VEP amplitude vs spatial frequency is plotted (Tyler *et al.*, 1978; and others). The precise shape of this function varies between subjects as shown in Strasburger *et al.* (1989), in Bach and Joost (1988), and in Fig. 1. There may be a bimodal function which is narrowly tuned, or a wide range of spatial frequencies may generate relatively attenuated signals. In general, the notch is encountered frequently in normal observers and is highly repeatable in any one individual. The effect has attracted attention because in the spatial frequency region which generates attenuated responses the normal relationship between signal amplitude and contrast does not hold, thus limiting the applicability of the VEP technique [a comprehensive table outlining the conditions under which a non-unimodal VEP vs spatial frequency function is obtained is provided in Strasburger *et al.* (1988)]. The data presented show that the notch, clearly evident with 8 Hz reversing gratings of contrast 40%, is absent if the same contrast and 16 Hz on–off presentation is used.

The principal component analysis of the pattern-reversal data shows that the variation between subjects can be ascribed to mainly two statistically independent sources which together account for 62% of the total variance. The remaining variance is split among many smaller factors and is, probably, best described as random fluctuation. It is remarkable to what extent the tested 18 spatial frequency variables are correlated. It is further remarkable, that a simple factor interpretation is obtained by orthogonal rotation (see Fig. 2). One factor represents the activity at low spatial frequencies, up to 3 c/deg, and the other factor represents activity at higher spatial frequencies, above 3 c/deg. The three common high loadings at the lowest spatial frequencies should not be taken too seriously since the signal amplitudes and signal-to-noise ratios are low at the ends of the visible spatial frequency range. The fact that each factor loads on a contiguous range of spatial frequencies shows that it can be characterized as representing spatially tuned activity. The two factors are uncorrelated and there is a sharp transition between the two.

The factors are interpreted as representing the activity of a sustained and a transient mechanism, respectively. The concept of two such detecting mechanisms was developed in psychophysics in the context of grating detection (van Nes *et al.*, 1967; Keesey, 1972; Kulikowski, 1971; Kulikowski and Tolhurst, 1973), was supported by electrophysiological single cell recordings, and was further developed in both areas. There is general agreement on the overall characteristics of the two mechanisms: low spatial frequency, rapidly moving stimuli are mediated by transient detectors whilst higher spatial frequency slow moving or static stimuli are mediated by sustained detectors [for reviews see Legge (1978) and Breitmeyer (1984), cf. also Hubel and Livingstone's (1989) review of P/M cell characteristics]. A quantitative model of detection mechanisms in the temporal frequency domain is provided by Anderson and Burr (1985).

There is further agreement that over an intermediate range of spatial frequencies (2–6 c/deg) the two mechanisms operate simultaneously and from this it can be deduced that, through signal cancellation, in this intermediate range a notch should occur in the mean response function. Our phase data (Fig. 3), as well as previously published data (Strasburger *et al.*, 1988; for a review see there), shows that phase, in the mean, is different by at least 360 deg between the two spatial frequency regions where the two mechanisms are most active. This implies that the two mechanisms have different phase characteristics. In the spatial frequency region where both mechanisms are active, the phase difference will undergo a change from 0 to 360 deg, the specific individual value depending on the relative strength of activation and on the specific phase response of each mechanism. Whenever the phase difference is within ± 60 deg of 180 deg, partial cancellation will occur.

Electrical cancellation hypotheses have been considered previously, and some counter arguments need attention. Various subsystems, e.g. retinal quadrants, have been proposed as possible explanations (see review in Strasburger *et al.*, 1988, p. 1082). What we consider here are subsystems which can be described on the basis of their spatial and temporal frequency response. Tyler *et al.* (1978, p. 547) rule out cancellation occurring with spatial frequency selective mechanisms on the ground that, for cancellation to occur, phase needs to be different by at least 120 deg *at the peaks* of the amplitude/spatial frequency function. There are, however, two implicit assumptions in this argument: that the mechanisms be narrowly tuned (otherwise phase at a peak will be contaminated by the other mechanism's phase) and, more importantly, that the mechanisms' individual phase responses are independent of spatial frequency. Our phase data in Figs 1, 3 and 4 contradict such a phase constancy. There are many subjects with a large overall phase variation, often several times the value of 180 deg. Consequently, we differ from these authors in that we say that at least one mechanism's phase depends on spatial frequency. This dependency will be different for each subject but there has to be an increase of varying degree with increasing spatial frequency. Therefore, any phase difference in excess of 120 deg between spatial frequency points somewhere either side of the notch leads to cancellation.

It would be interesting to further specify the amplitude and phase characteristics of the mechanisms' response from our data. However, although it is simple to predict how two specified mechanisms will superimpose, there is no simple solution for the inverse problem of specifying the mechanisms' responses from the overt response.* For example, overt phase at the peaks needs not be that of the mechanisms, and the broadness of overt peaks and of the underlying channels may be different. The sharp tuning found in the PCA does not imply that the mechanisms themselves are sharply tuned. It should further be remembered that the present model is still too simple to account for steady-state VEP data in general. Tyler *et al.* (1978) already show the high complexity of VEP responses. Consequently, different numbers of mechanisms have been proposed for the pattern-reversal VEP. Tyler *et al.* (1978) and Tyler

*When phase is variable for one mechanism and is, for simplicity, assumed to be a linear function of spatial frequency, there are at least eight parameters to be determined: peak sensitivity, bandwidth, and phase offset for the two channels, phase slope for one channel, and peak separation.

and Apkarian (1985) conclude that multiple (e.g. eight) pattern-specific mechanisms must exist. Strasburger *et al.* (1988) conclude that four mechanisms account for their data. However, these studies also cover more independent variables than the present one which is mainly concerned with the effects of spatial frequency and modulation mode. Tyler and Apkarian's (1985) eight mechanisms cover the effects of spatial frequency, contrast, and ocularity (they also assume "at least two spatial frequency regions", p. 765), and Strasburger *et al.* (1988) look at the effects of spatial frequency and contrast.

Finally, one might ask whether the difference in the VEP response is due to the difference between on–off and reversal, or due to the different temporal modulation frequencies. The question is ill-posed, however: since the overall process leading to an evoked potential is nonlinear, different modulation modes cannot be directly compared. A specific aspect of this is discussed in the Appendix, namely which frequency components should properly be compared between reversal and on–off (the on–off component which corresponds to the second harmonic in 8 Hz pattern reversal might either be the 8 Hz on–off second harmonic or the 16 Hz on–off fundamental). For the present analysis, however, such a comparison is not required. Empirically, the above posed question, whether the absence of notches in the 16 Hz on–off response stems from the higher modulation rate *per se* and would also occur in pattern reversal modulation, can be answered from the literature. Tyler *et al.* (1978) demonstrate the high interindividual response variability and sharp tuning for pattern reversal over a wide range of temporal frequencies (including 16 Hz), very unlike the responses which we obtained for 16 Hz on–off.* Further, any explanation for the differences in VEP response must also take into account the differences which we found between pattern reversal and on–off at 8 Hz modulation rate.

Onset presentation

On–off stimulation has previously been described as being a less efficient stimulator of transient mechanisms (Kulikowski and Tolhurst, 1973), and we find this confirmed by our present results. The principal component analysis, for the 16 Hz on–off data, yielded an overwhelming influence of a single factor (61% of the total variance). Consequently, this factor loaded over a broad range of spatial frequencies. The contrast sensitivity data in Fig. 6 provides evidence as to what kind of mechanism that is. The data indicate that on–off presentation at 16 Hz only weakly stimulates transient mechanisms because, at low spatial frequencies where these are most sensitive, sensitivity to the 16 Hz on–off stimulus is poor. The low activation of the transient mechanism by 16 Hz on–off might seem surprising, given the high temporal frequency. It is, however, well known that the transient system has a band-pass characteristic; Anderson and Burr's (1985, Fig. 5) data show that 16 Hz is beyond the peak of this function which is around 10 Hz, so the high temporal frequency does not bring an advantage in transient stimulation. Sensitivity of the transient channel at 16 Hz is, according to Anderson and Burr's model, reduced relative to 8 Hz by a factor of between 1.4 (at 1 c/deg) and 2.2 (at 10 c/deg). According to the same model, the sustained mechanism is also reduced in sensitivity at 16 Hz relative to 8 Hz (by a factor of 1.95 at 1 c/deg and by 2.1 at 10 c/deg), so the sensitivity reduction is roughly equal for the two mechanisms. Now, the 16 Hz on–off stimulation in the present experiments, having the same maximal contrast as the pattern-reversal stimulus, has a contrast *change*, which is only half that of the reversal stimulus. Since it is contrast change that determines the activation of the transient system (cf. Kulikowski and Tolhurst, 1973), transient activation from the on–off stimulus is only half that of the pattern-reversal stimulus (in linear systems theory, a system which is sensitive to a *change* in the input signal is said to have *differentiating* behaviour). The conclusion, from the PCA analysis and from the sensitivity data in Fig. 6, that the 16 Hz on–off stimulus only weakly activates the transient mechanism, is thus in agreement with Anderson and Burr's model.

In further agreement with this interpretation, the VEP data of Figs 1 and 3 for 16 Hz on–off presentation at 40% contrast show that the notch is absent in all subjects who exhibited a notch with contrast-reversal stimulation. At higher contrasts, in some subjects a notch is evident in the 16 Hz data. In these cases, an

*One of their four subjects shows, at 16 Hz, the disappearance of a notch which is evident at lower temporal frequencies, between 8.5 and 14 Hz (1978, Fig. 7). This disappearance is confined to a narrow range of temporal frequencies (14–15.6 Hz).

additional activity peak builds up at low spatial frequencies. This is to be expected from the foregoing, i.e. contrast change is now sufficient to stimulate the transient mechanism at its point of highest sensitivity (Kulikowski and Tolhurst, 1973) to the extent that its activity is apparent in the VEP. Such a concept of a balance between transient and sustained mechanisms has already been described by Kulikowski (1975).

If as asserted above, the 8 Hz reversing gratings are a particularly effective stimulus for transient mechanisms then they should have very high contrast sensitivity at low spatial frequencies. The data in Fig. 6 show that this is indeed the case; the 8 Hz contrast reversing stimulus is detected more easily at low spatial frequencies than either 16 Hz on–off or 8 Hz on–off.

The 8 Hz on–off stimulus plays an intermediate role between 16 Hz on–off and 8 Hz reversal. It is more easily detected at low spatial frequencies than 16 Hz on–off, as seen in the psychophysical data (Fig. 6), and as such is a less pure stimulator of sustained mechanisms. Again, this is in agreement with the proposed generation mechanism. However, we have no explanation for the inter-subject variability and for the lack of a systematic pattern in the amplitude function. There is often a region of attenuated amplitude and a loose resemblance to the reversal response but the amplitude fluctuates markedly with spatial frequency. One might think of a variable superposition of onset and offset responses (cf. Estévez and Spekreijse, 1974) or of non-linear interactions between the alpha rhythm and 8 Hz VEP activity (note that *linear* superposition cannot be an explanation). At the moment we just wish to point out these results since 8 Hz on–off modulation, with *sinusoidal temporal waveform*, has to our knowledge not been tried before. Interestingly, the phase is particularly stable (Figs 1 and 2) and resembles the phase response for the 16 Hz on–off stimulation. Bearing in mind the comments about temporal modulation frequency made above, it may be that the interpretational problems posed by 8 Hz on–off could be resolved by investigating a range of temporal frequencies. This issue forms part of a series of different experiments at present being carried out.

Temporal phase response

For the transient VEP it is well known that latency can be determined to a high degree of intra- and inter-individual stability with standard deviations below 10%. The corresponding parameter in the steady-state VEP, temporal phase, shows a similar stability. This is strikingly evident from Fig. 2 which shows low inter-individual variation.

The fact that, for pattern reversal, the mean phase is markedly different between those spatial frequencies where the two mechanisms are most active shows that the mechanisms have different phase characteristics, i.e. the increase in phase with increasing spatial frequency reflects the increasing contribution of a second, slower mechanism active at higher spatial frequencies. This also explains why we often find an abrupt increase in phase around 3 c/deg [Fig. 3(a, b)]. The phase levels of 270 and 690 deg [Fig. 2(b)] may represent the operation of these two mechanisms which differ by approx. 420 deg. This corresponds (at 16 Hz) to a difference of 70 ms. A second source for an increase of pattern-reversal phase with increasing spatial frequency seems to be an increase of phase of one of the mechanisms (the transient, see below) itself, since phase often continues to increase beyond the activity peak, whereas constant phase for both mechanisms would produce an ogive-shaped phase function.

The phase data in the case of 16 Hz on–off stimulation [Fig. 3(c)] is nearly perfectly independent of spatial frequency. This phase response thus appears to represent the activity of a homogeneous group of detectors, probably a sustained-like mechanism. Its phase can be assigned to 270 deg, as shown in the figure, or to 270 deg + 360 deg = 630 deg. Although, in the figure we have chosen to assign it to 270 deg for lack of absolute phase information, choosing a value of 630 deg is more consistent with our interpretation that it is reflecting sustained activity as this is close to the value of 690 deg found for the reversal stimulation at higher spatial frequencies [Fig. 2(b)]. [Recording at a fixed temporal frequency can only yield relative temporal phase; absolute phase assignments can be made by using a range of temporal frequencies (Diamond, 1977).] Summarizing, the sustained mechanism, being most active at higher spatial frequencies, seems to have a longer latency which is independent of spatial frequency and the transient mechanism's phase seems to have an overall increase with spatial frequency.

The high phase stability for 16 Hz on–off stimulation [Fig. 2(c)] has two *practical implications*. First, based on the low inter-individual variance, the phase for this modulation type can be used as a purely descriptive measure of normal visual functioning, much like the use of transient VEP latency. Since SSVEP phase shares many properties with transient latency, such as having similar dependency on spatial frequency and contrast (Strasburger *et al.*, 1988), phase can also be expected to react similarly to diseases known to affect the VEP. Indeed, Kupersmith *et al.* (1984) have shown the effectiveness of the SSVEP in detecting visual pathology in multiple sclerosis. The higher recording speed of the SSVEP allows a wider range of spatial frequencies to be examined thus allowing it to detect spatial-frequency-specific losses. The occurrence of such losses has been reported frequently (e.g. Regan *et al.*, 1977; Rentschler *et al.*, 1982) and their detectability by means of the SSVEP has been demonstrated by Kupersmith *et al.* (1984).

Secondly, high phase stability allows the application of phase-locked VEP recording (Nelson *et al.*, 1984b; Wiener *et al.*, 1985; Strasburger, 1987; Peli *et al.*, 1988; see also Norcia and Tyler, 1985). Phase-locked recording can significantly improve the signal-to-noise ratio or can reduce recording time. High speed data acquisition is particularly desirable in a clinical setting yet the applicability of phase-locked analysis is limited when reversal stimulation is used because phase varies with spatial frequency and contrast. Here, a further advantage of 16 Hz on–off stimulation emerges; Figs 1–4 show the relative invariance of phase which means that with this form of stimulation, phase-locked data extraction techniques will have much wider applicability.

The SSVEP as an index of visibility

VEP measures of contrast threshold. The VEP has provided the basis for several non-invasive objective techniques of assessing visual function. Previous attempts at relating VEP data to subjective measures of visibility have followed two approaches. One method is to compare contrast thresholds of VEPs and psychophysical detection, either by extrapolation from the VEP for a range of suprathreshold contrasts (Campbell and Maffei, 1970) or by Cannon's (1983) method of constant near-threshold amplitude (for a review see Cannon, 1983; Strasburger *et al.*, 1988). In the present report we confirm the validity of the regression technique. We also show that thresholds predicted from the 16 Hz on–off data are similar to those obtained with 8 Hz reversal modulation. The advantages of on–off arise from the smoothness of the spatial tuning function (see Figs 1 and 3) which permits applying the regression technique also in cases where pattern-reversal data is noisy. This allows accurate determination of psychophysical thresholds.

All VEP thresholds in our experiments are offset from psychophysical thresholds by *c.* 0.8 log units. Threshold over-estimation (i.e. sensitivity under-estimation) by the VEP, though smaller, has been reported before (Cannon, 1983, *c.* 0.5 log units; Nelson *et al.*, 1984a, *c.* 0.6 log units; Tyler and Apkarian, 1985, *c.* 0.5 log units). There are, however, also reports of VEP thresholds being equal or possibly even below subjective thresholds (Allen *et al.*, 1986; Strasburger *et al.*, 1988; Norcia *et al.*, 1989). We suspect that these different observations are related to methodological differences. The main part of the difference probably stems from the criteria applied when a VEP signal is considered to be above noise. Including low amplitude signals means that phase information must be involved in this decision process. In Allen's study, amplitude vs contrast functions were obtained by direct contrast sweeps whereas in the present study these functions were inferred from spatial frequency sweeps taken at several contrast levels. Consequently, it was necessary for phase to be reliable over a period of up to 2 h, whereas in Allen's study such reliability was only required during the 10 s duration of the sweep. Note that low-contrast activity, accepted as signal by virtue of its phase coherence, will have a shallower slope than that part of the amplitude/contrast function on which we have based our regression. As a further difference, adaptation might have played a different role in the present study (cf. Nelson *et al.*, 1984b). Although we took care to let subjects rest between sweeps, and a certain amount of rest was also provided by the 1 s pause between stimuli, the 1 s stimulus presentation prior to each VEP acquisition is likely to have caused some adaptation. We suspect this effect to be small, however, since unlike in the case of downward contrast sweeps considered by Nelson, the stimulus pre-presentation in our case was *at* the contrast level of the stimulus proper. A final difference between Allen's and the present study is our use of a lower stimulus luminance (17 cd/m^2 as compared to 80 cd/m^2).

An alternative approach aimed at relating VEP data to subjective measures is to avoid the regression technique and make a direct comparison between the shape of the VEP amplitude vs spatial frequency response and the contrast sensitivity function (Levi and Harwerth, 1978; Pirchio *et al.*, 1978; Fiorentini *et al.*, 1980). Some authors found the similarity between these two curves so striking that they renamed the vertical (amplitude) axis as sensitivity (Pirchio *et al.*, 1978; Fig. 2). There is a conceptual as well as an empirical difficulty with this approach, however. Empirically, the slope of the VEP amplitude vs contrast function, which can be regarded as an index of gain or responsiveness of the underlying contrast processing system, can be quite unrelated to the threshold, i.e. the intersection with the contrast axis. Conceptually, VEP amplitude is a response-related measure valid for a range of suprathreshold contrasts whereas the contrast threshold is a stimulus-related measure specifying one extreme point on the contrast axis. The gap between these two domains can be bridged when certain assumptions are met: (a) linearity of the VEP amplitude/log-contrast function, (b) independence of this function's slope from spatial frequency and (c) absence of saturation (Strasburger *et al.*, 1988; Fig. 9). We have assessed the validity of these assumptions for 16 Hz on–off stimulation in three subjects (AR, KC, RV): for the range of spatial frequencies tested the amplitude/log-contrast function is approximately linear [criterion (a)] and its slope is sufficiently independent of spatial frequency [criterion (b)] as can be seen from Fig. 5. Figure 4 illustrates that saturation is absent below 55% contrast [criterion (c)]. Since these criteria are met, we consider it appropriate to do a least-squares fit of VEP amplitude to mean log contrast sensitivity. This is shown in Fig. 8. The solid symbol curve shows the mean CSF for the four subjects from Fig. 7, the open symbol curve repeats the mean normalized VEP amplitude data for the same four subjects from Fig. 7. A linear scale transformation was applied to the VEP data to obtain a least-squares fit to the CSF data. The transformation, for our data, was given by

$$A' = 0.0128A + 0.92$$

where A' is predicted psychophysical threshold in log percent, and A is normalized VEP amplitude in percent. It is evident that with normalization (as in Fig. 3) and with this transformation applied, the two curves are strikingly similar. Before such a method can be universally adopted, however, the robustness and the valid range of the employed scale transformation has to be tested. For example, predictions are only possible for non-zero positive VEP amplitude since $A = 0$ still predicts a threshold of 0.92 (8.3% contrast, in good agreement with our threshold offset described earlier). Note also that the maximum voltage of VEP amplitude is quite different between subjects so that different scaling factors are used in the normalization procedure and only relative rather than absolute sensitivity can be determined in this way.

The VEP as a measure of contrast perception. In the previous section we have been concerned with the relationship between VEP activity and contrast thresholds. The VEP is necessarily generated by suprathreshold contrast, however, and in this section we consider the relationship between VEP amplitude and suprathreshold contrast perception using the concept of apparent contrast as described by Blakemore *et al.* (1973) and Georgeson and Sullivan (1975). One difficulty with this approach is that the VEP amplitude vs spatial frequency function is an inverted-U shape whereas apparent contrast, as described by Georgeson and Sullivan (1975), is independent of spatial frequency, i.e. the plot is virtually a straight line (Georgeson and Sullivan, 1975, Figs 1 and 2). Kulikowski (1976a, Figs 3(b) and 11), however, has shown that the perceived suprathreshold contrast function is actually curved, the curvature being under emphasized by Georgeson and Sullivan's use of a logarithmic scale. A log scale will emphasise differences occurring at low values (i.e. near threshold) and will reduce differences occurring at high values. Kulikowski (1976a) further showed that with linear scaling the apparent

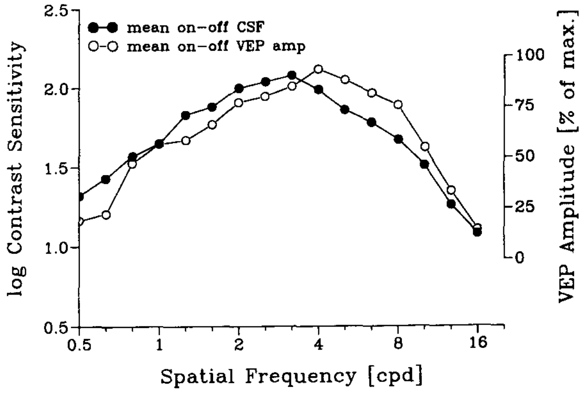

Fig. 8. Mean normalized VEP amplitude for on–off 16 Hz modulation, fitted to mean 16 Hz on–off contrast sensitivity from Fig. 7.

contrast function has the same shape as the CSF and can be modelled as being the sum of threshold contrast and physical contrast.

Based on iso-apparent-contrast curves (i.e. curves of constant contrast) reported by Blakemore *et al.* (1973, Fig. 7) we have calculated apparent contrast as a function of spatial frequency; this is shown in Fig. 9(a). The 20% curve is derived by interpolation between Blakemore's 7 and 22% curves, averaged between the two subjects, and the 40 and 60% curves are derived by interpolation between 22 and 70%. As can be seen from the figure, the three curves have similar shape and can indeed be modelled as being offset by a constant additive value from each other, as predicted by Kulikowski. The corresponding VEP amplitude curves from Fig. 4 are shown next to these [Fig. 9(b)]. The differences between the psychophysical and VEP data are as follows. The VEP data show a pronounced peak around 4 c/deg which is not evident in the psychophysical data. The VEP data have a much greater dynamic range than the psychophysical data as illustrated in the figure for the 60% curves. As a consequence, no transformation of VEP data can lead to a match with the psychophysical data. Taking, for example, the logarithm of the VEP data has the effect of flattening the VEP curves but also shifts the three curves closer together. (Obviously, better matching would be obtained if each curve were fitted separately, using different transformation parameters for each but this procedure is conceptually and physiologically meaningless.) Stated differently, the apparent contrast functions can be well modelled using an *additive* offset, whereas the VEP amplitude functions can be better modelled using a *multiplicative* offset.

Thus, although both these measures relate to suprathreshold contrast, VEP amplitude and perceived contrast functions do not match. The discrepancy may be due to a lack of association between the number of neurons activated and contrast sensation. It might be that for very low and high spatial frequencies the number of contributing neurons is too small to evoke significant surface potential, whereas it is sufficient to lead to a contrast sensation. Furthermore, the suprathreshold matching experiments (Blakemore *et al.*, 1973) were performed using static gratings whereas VEPs are obtained from temporally modulated gratings. Given the differences in the underlying transient and sustained detecting mechanisms it is likely that apparent contrast will also be different in these cases.

Separating transient and sustained mechanisms with the VEP—other studies

There have been several attempts at separating sustained and transient subsystems using

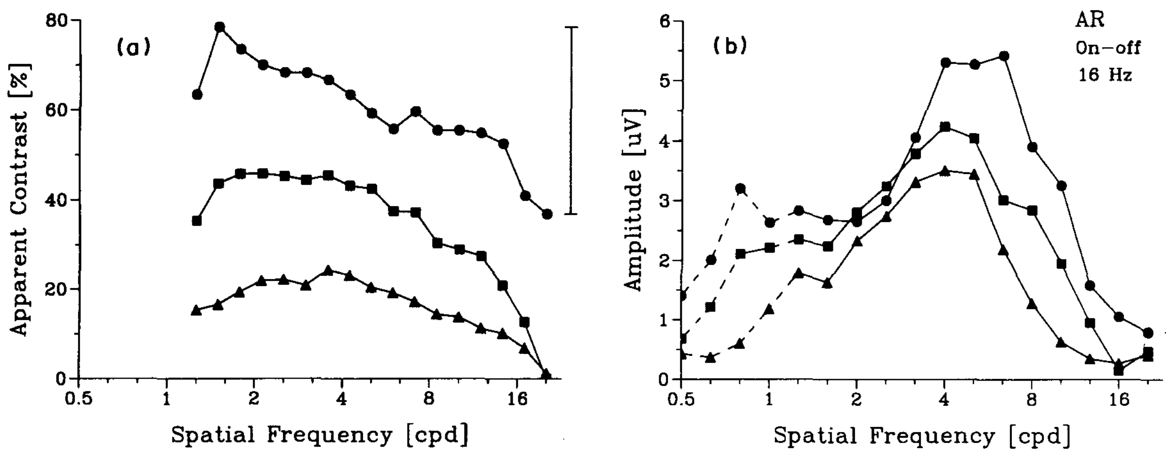

Fig. 9. (a) Apparent contrast of sine-wave gratings of 20, 40 or 60% physical contrast. Data have been calculated based on iso-apparent contrast curves shown by Blakemore *et al.* (1973, Fig. 7). These authors have matched in contrast sine-wave gratings of different spatial frequencies to a reference grating of 5 c/deg which had either 7, 22 or 70% physical contrast (field size 4 × 3 deg, 4.8 cd/m^2). The 20% curve is obtained by interpolation between Blakemore's 7 and 22% curves, the 40 and 60% curves by interpolation between 22 and 70%. (b) VEP amplitude data for subject AR, replotted from Fig. 4, for comparison. Data points from Fig. 4 below 1.2 c/deg are joined by dashed lines in order to facilitate the comparison to (a). The vertical bars in (a) and (b) denote the dynamic ranges for the 60% curves to illustrate their difference.

the VEP. Nelson *et al.* (1984a), for example, used the oblique effect, other techniques have attempted to exploit the onset–offset mode of stimulus modulation. In the so-called difference technique, transient VEPs evoked by on–off modulated and contrast-reversing gratings are recorded and the reversal response is subtracted from the onset response (i.e. without the offset response) (Kulikowski, 1976b, 1977b, 1978; Murray and Kulikowski, 1983). The amplitude of this difference trace is regarded as being an index of the activity of the pattern system, whereas the reversal response is regarded as being dominated by the movement system. The corresponding contrast thresholds are determined by regression to zero voltage. In another line of work (Bain and Kulikowski, 1976; Murray and Kulikowski, 1983) steady-state VEPs elicited by either on–off or pattern-reversal modulation are recorded over a wide range of contrast values; separate regression lines are then fitted to the high and low contrast range separately. Extrapolation to zero amplitude of the high-contrast limb is considered to reflect transient activity whereas for the low contrast limb it is considered to reflect sustained activity. [For psychophysical evidence for low and high contrast mechanisms see, e.g. Burbeck and Kelly (1981), Harwerth and Levi (1978) and Harwerth *et al.* (1980), for a review see Breitmeyer (1984).] A similar separation into a high and low contrast mechanism as evidenced by SSVEPs has been proposed and their characteristics described by Strasburger *et al.* (1988, p. 1083).

Like these authors, we have found that the subtraction technique, which seems to be successful for transient VEPs, does not generalize well to the steady-state case. Our 8 Hz on–off amplitude data is too variable between subjects to be meaningfully compared with pattern-reversal responses at this same presentation rate (8 Hz modulation, i.e. 16 reversals per s). The two-limb regression technique, however, seems to have a basis compatible with the present results. We did, indeed, find many cases where two, rather than a single straight line were required to describe the amplitude vs contrast plot. In these cases, the slope at higher contrast was always steeper than that at low contrast so that, for higher contrast, a higher extrapolated threshold was obtained. The cases of two slopes occurred always at low spatial frequency where the simultaneous operation of sustained and transient mechanisms is most likely. Yet using this technique to systematically separate transient from sustained activity has the difficulty that in the range below *c.* 2 c/deg, the two slopes were not *always* present, thus limiting the applicability of this approach.

CONCLUDING COMMENTS

Many applications of the pattern reversal VEP technique depend on the tenet that the amplitude of the response is linearly related to log contrast. As has been shown previously, however, in many subjects, the VEPs generated by contrast reversal have very low amplitude for certain spatial frequencies resulting in a region of low amplitude in the spatial frequency vs amplitude function. A principal component analysis of the VEP amplitude data shows that two independent sources contribute to the variation over subjects, and that these sources possess the characteristics of transient and sustained mechanisms. Although a model based on two mechanisms cannot account for the high complexity and interindividual variability of the steady-state VEP response in general, up to 70% of the intraindividual variability in the present data can be attributed to their influence. Further, the notch in the amplitude function can be explained to be a result of interactive effects between these mechanisms, be they of neural inhibitory origin or representing superficial electrical signal cancellation. On–off stimulation, which is known to be a less effective stimulus for transient mechanisms than the widely used contrast reversal, leads to weaker interactive effects between transient and sustained mechanisms and may thus be particularly useful in diagnostic assessment of spatial visual function.

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APPENDIX

Conceptual Differences Between On–Off and Reversal

Which frequency component?

Comparing on–off and reversal modulation raises the question of which temporal frequency components should properly be compared. We believe that the answer to this question depends on how it is considered these stimuli are processed by the visual system so that the question cannot be answered satisfactorily at this time. An on–off modulated grating can be decomposed into a static and modulated grating superimposed:

$$I_{oo} = I_{mean}(\tfrac{1}{2} + \tfrac{1}{2}C_m \sin \omega_x x) + I_{mean}(\tfrac{1}{2} + \tfrac{1}{2}C_m \sin \omega_t t \sin \omega_x x). \quad (3)$$

Disregarding the static component it seems natural to compare only the pattern reversing components of the two stimuli. That is, the fundamental (and second harmonic) components of the on–off and reversal stimuli should be compared. In the case of reversing stimuli there is, however, no signal energy at the fundamental frequency of the contrast reversal stimulus whereas there is significant activity at the fundamental in the on–off case. Hence this approach is unsatisfactory. Perceptually, the two temporal half-cycles in pattern-reversal are similar (a grating appearing in each half cycle) whereas they are dissimilar in the on–off case (a grating either appearing or disappearing).

An alternative approach is to describe a pattern-reversing grating as an on–off grating which changes its phase with each appearance:

$$I_{rev}(x,t) = I_{mean}(1 + C_m|\sin \omega_t t|\sin(\omega_x x + \varphi)), \quad (4)$$

where phase φ alternates between 0 and ω according to

$$\varphi(t) = \begin{cases} 0 & 0 \leqslant t < \pi/\omega_t \\ \pi & \pi/\omega_t \leqslant t < 2\pi/\omega_t. \end{cases}$$

According to this view it is natural to compare the appearance–disappearance rates of the two kinds of stimulation. The appearance rate of pattern reversal [equation (4)] is the absolute value of $\sin \omega_t t$ which is twice the fundamental frequency. For an on–off modulated grating, on the other hand, the appearance rate is simply the modulation frequency. Hence, in this view, the second harmonic of the reversal is comparable with the fundamental of the on–off stimulation.

Static appearance of on–off

At high temporal frequencies on–off gratings appear similar to static gratings. This may be due to temporal integration. Unlike reversing gratings, on–off gratings contain a component of standing contrast of $\tfrac{1}{2}C_m$. Integrating relationships (2) over time shows that contrast averaged over time is zero for reversal but $\tfrac{1}{2}C_m$ for on–off:

$$\frac{1}{T}\int_0^T C_{rev}(t)\mathrm{d}t = 0 \quad \text{and} \quad \frac{1}{T}\int_0^T C_{oo}(t)\mathrm{d}t = \tfrac{1}{2}C_m \quad (5)$$

where T is the temporal period $T = \omega_t/2\pi$.

Kulikowski and Tolhurst (1973) showed that contrast sensitivity to a reversing grating is twice that to an on–off grating. This was considered to be due to the fact that the physical contrast change in reversal is twice that in on–off. Differentiating relationships (2) shows this physical property to hold:

$$\mathrm{d}C_{rev}/\mathrm{d}t = C_m \cos \omega_t t \quad \text{and} \quad \mathrm{d}C_{oo}/\mathrm{d}t = \tfrac{1}{2}C_m \cos \omega_t t. \quad (6)$$

Is there a rectification stage in the visual system?

For reversal stimulation, only the second harmonic (i.e. 16 Hz) is reported. The first harmonic, as others have noted, shows no relationship to the stimulus. This is often taken to reflect the activity of some kind of rectifying stage along the visual system's signal path (for a review see Regan and Spekreijse, 1986). Such a rectification stage is often, for separate reasons, included in psychophysical models, for example in Watt and Morgan's MIRAGE model (Watt and Morgan, 1985). As an aside, it is interesting to note that the VEP frequency doubling could be based on a different kind of non-linear behaviour. Inspecting equation (4) shows that if the spatial phase information φ, i.e. the absolute horizontal grating position, is not retained in the VEP generating process, then only multiples of $2f_t$ can occur. Since small eye movements during the recording are inevitable and even necessary for the image not to fade, this might be a plausible alternative explanation for the frequency doubling effect.