BINOCULARITY IN THE HUMAN VISUAL EVOKED POTENTIAL: FACILITATION, SUMMATION AND SUPPRESSION

PATRICIA A. APKARIAN, KEN NAKAYAMA and CHRISTOPHER W. TYLER

The Smith-Kettlewell Institute of Visual Sciences, 2232 Webster Street, San Francisco, Calif. 94115 (U.S.A.)

(Accepted for publication: September 30, 1980)

The discovery of single cortical neurons responding to similar visual inputs to the two eyes, yet selectively sensitive to particular amounts of binocular disparity (Barlow et al. 1967; Pettigrew et al. 1968), has provided an important advance in the investigation of binocular vision and stereopsis. Although recent experiments differ on important details (Poggio and Fischer 1977; Fischer and Krüger 1979), there is unanimity regarding the existence of neurons with differing amounts of preferred disparity. Such cells, for example, produce large responses only at an optimal binocular disparity, and in some studies this preferred disparity differs from cell to cell. Furthermore, the response at this optimal disparity is often very much larger than the sum of the responses obtained from stimulation of each eye separately. Thus it appears that there can be a considerable degree of binocular facilitation in cortical cell responses and that the presence of neural facilitation may be related to the processes of stereopsis.

The characteristics of human binocular facilitation with corresponding binocular stimuli are the main focus of our study. We wished to establish the nature of such facilitation before progressing to the effects of binocular disparity, which require a further level of technical sophistication.

In the field of visual evoked potentials (VEPs), however, it has been difficult to obtain data which can be considered analogous to the results obtained from single units, despite the fact that a large number of VEP studies have been concerned with binocular interaction. A major problem of the binocular evoked potential studies is that variations across laboratories both in the recording techniques and in the stimulus conditions have resulted in conflicting reports as to the degree and type of binocular interactions which exist (see next section for definitions). As a result, the range of binocular interactions reported in the literature is from zero summation (Inoue 1966) to small amounts of facilitation (Cigánek 1970; Srebro 1978), with most authors reporting at least partial summation (e.g., Gouras et al. 1964; Perry et al. 1968; White and Bonelli 1970; Harter et al. 1973). The rarity of binocular facilitation observed in the VEPs is in strong contrast to the frequent binocular facilitation revealed with single unit research (Barlow et al. 1967; Pettigrew et al. 1968; Poggio and Fischer 1977; Von der Heydt et al. 1978).

One possible reason for the dearth of binocular facilitation in previous VEP studies is the presumed inability of the VEPs to selectively record from small subsets of cortical neurons having the same disparity, orientation

1 Supported by NIH Grants No. 5R01 EY01582, 1R01 EY02124, 5P30 EY01186; NIH Biomedical Research Support Grant No. 5S01 RR05566; and The Smith-Kettlewell Eye Research Foundation.

2 To whom reprint requests should be addressed. Present address: The Netherlands Ophthalmic Research Institute, P.O. Box 6411, 1005 EK Amsterdam, The Netherlands.
and spatial frequency tuning. As such, the wide range of stimulus-response functions (characteristic of single units) would be obscured when recordings are made from many different types of neurons at once. If one takes this view, the lack of binocular specificity seen in the VEP is less surprising.

Our own work questions this interpretation of VEP recording, however, because we have found that the steady-state human VEP amplitude is very sensitive to remarkably small changes in stimulus characteristics. For example, when the VEP amplitude is measured as a function of spatial frequency, the resulting functions are very sharply tuned, showing multiple-peaked bandpass characteristics which are much steeper than the psychophysical contrast sensitivity curve (such functions are replicated in this paper and can be seen in Figs. 3, 4, etc.). In fact, parts of the narrow spatial frequency tuning functions are more similar to those obtained from single cell recordings, rather than that expected from a representative population of neurons tuned to a wide range of pattern size. Furthermore, the temporal tuning of these responses is even sharper than the spatial tuning.

As yet, we have no firm understanding as to how the seemingly unspecific technique of VEP recording can isolate small populations of neurons. However, observations on the phase of the VEP (Tyler et al. 1978) and the ability to selectively isolate single peaks (Nakayama et al. 1981) indicate that the results are not an artifact of electrical summation or the inhibitory interaction of more broadly tuned mechanisms. What is clear is that this isolation of small subsets of cortical neurons is a prominent feature of VEP recording and should be recognized as such.

Our guiding hypothesis, therefore, has been that past discrepancies within the binocular VEP literature, as well as between evoked potential and single unit studies are due to the existence of this peculiar sampling characteristic of the VEPs.

Consideration of the detailed tuning of the VEPs suggested that a similarly fine-grained analysis would be necessary for a full examination of binocularity in the human VEP. This paper reports such an analysis, to provide the basis for resolving some of the contradictions of previous VEP work, and to relate the results to those obtained from single units.

The aim of the study was therefore to determine the degree of binocular facilitation that could be measured in the VEP for a wide range of conditions of spatial frequency, temporal frequency and contrast of sinusoidal pattern stimulation. We then selected the regions of greatest binocular facilitation to determine whether they were affected by the presence or absence of binocular fusion.

Binocular interaction terminology

Inconsistent terminology used to describe various types of binocular interactions has resulted in additional conflict within the VEP literature. To reduce confusion, binocular interaction terminology used in this study is outlined below.

We define 3 regions of binocular summation delineated by two boundaries, each of which may indicate different underlying processes. These regions are based on the empirically validated assumption of the absence of electrical cancellation due to temporal phase differences in the responses from the two eyes (see e.g., Fig. 5).

The levels of binocular interaction are expressed numerically in terms of the binocular amplitude (B) in relation to the mean monocular response (M).

1. Inhibition (B < M). The amplitude of the binocular response is less than the mean of the two monocular responses. This situation is typically restricted to observers with unequal binocular vision. It represents inhibition of the response from one eye by stimulation of the other.

2. Zero summation (B = M). The binocular response should be equal to the mean monocular response in normal observers in situations of binocular rivalry, where the output represents the response from each eye alternately. In non-rivalrous situations, another possible
mechanism for this result is suppression of the monocular responses by the stimulation of a separate binocular mechanism. Depending on the relative strength of the mechanisms, zero summation could result. This level of summation is therefore inconclusive as to the underlying interactions.

(3) Partial summation ($M < B < 2M$). Failure to exhibit full summation implies the absence of independence between the two eye responses, but little more. A binocular system, for example, could saturate or the degree of interaction could be a more complex function, given the existence of both monocular and binocular mechanisms.

(4) Summation ($B = 2M$). Due to electrical additivity, the binocular response will equal the sum of the two monocular responses if the information from the two eyes is independent. It is also possible to envisage either a linear binocular mechanism or a combination of binocular and monocular mechanisms which could produce the same result.

(5) Facilitation ($B > 2M$). The binocular response can be greater than the sum of the monocular responses only if there is some kind of facilitatory binocular interaction. This could be in the form of a binocular mechanism in addition to the monocular mechanism, or some other preferential response to binocular stimulation. We presume that binocular facilitation has some relationship to the presence of a neural stereoscopic depth mechanism.

**Methods**

**Stimulus**

Sinusoidal gratings modulated in counterphase at various spatial frequencies were generated in the conventional manner on the face of a Hewlett-Packard cathode ray tube (CRT) display (Model 1332A, P31 Phosphor). The space average luminance was kept constant at 46 cd/m², unless otherwise specified, and contrast was measured according to the standard Michelson (1927) definition. All light measures were made with either a calibrated selenium photocell or a Spectra Pritchard photometer (Model 1980A).

The stimulus patterns which were typically vertical gratings were reflected onto a front surface mirror to be viewed by the observer (except in the stereopsis studies which involved variable stimulus orientation and dichoptic stimulus presentations). During the stereopsis studies, one eye viewed the mirror image of either a vertical or horizontal grating through a dove prism which was properly aligned to assure zero stimulus disparity, while the fellow eye viewed the image directly. The decrease in apparent distance introduced by the dove prism was only 1.9 cm or 3.3% of the viewing distance. Horizontal gratings under binocular viewing conditions were obtained by rotating the CRT display 90°. For dichoptic viewing, i.e., horizontal to one eye, vertical to the other, the dove prism was rotated 45°. Care was taken to insure optical alignment about the center of rotation.

**Recording and data analysis**

Bipolar recording was employed with one of the recording electrodes placed 3 cm above the inion and the other 3 cm to the right of the first; the ground electrode was placed on the ear lobe. We chose this electrode configuration since it has been found to be optimal for pattern evoked potentials (Cobb et al. 1967; Jeffrey and Axford 1972).

Amplified EEG signals were prefiltred through a Krohn-Hite (Model 330M) 24 dB/octave bandpass filter with cut-off frequencies set at 0.1 log unit above and below the pattern reversal rate and then analyzed by means of a synchronous narrow-band filtering technique similar to that described by Fricker (1962). Steady-state visual evoked potentials were obtained with two types of recording conditions. (1) Under discrete recording conditions, one spatial frequency at a time was presented for 10 sec. The prefiltred EEG signals were passed through a synchronous narrow-band (0.03 Hz) commutating filter cen-
tered on the stimulus reversal frequency. The responses were integrated over the 10 sec recording epoch, rectified and the results displayed on a digital counter. (2) Under continuous recording conditions, counterphase flickering gratings were continuously varied in spatial frequency from 0.2 to 20 c/deg over 20 sec. In this condition, the sweep method recently described in more detail by Tyler et al. (1979), the signals passed through a filter of approximately 0.57 Hz bandwidth, the output of which was rectified and plotted on the Y axis of an X-Y plotter. The X position was determined by the ramp producing the frequency sweep. Further details of our recording and data analyses procedure are published elsewhere (Tyler et al. 1978, 1979).

To distinguish neural activity evoked by the stimulus from uncorrelated background activity at the stimulus frequency, the evoked potential amplitudes are expressed in signal-to-noise ratios (with the exception of raw data presentations). The average noise level for a given temporal frequency was obtained by recording the response to a homogeneous field at random intervals during each recording session. The mean signal amplitude for each stimulus condition was then divided by the empirically determined noise amplitude (except in the study on binocular interactions and temporal frequency).

The average noise level smoothly attenuates (approximately 1 decade) across a wide range of temporal frequencies and can typically be fitted by a theoretical filter function having a slope of \(-1\) (Tyler et al. 1978). For comparisons across temporal frequency, signal-to-noise ratio expressions of response amplitude compensate for the resultant attenuation. For observer AH, noise values as a function of temporal frequency were obtained (Fig. 1) for comparisons with his spatial frequency tunings which were studied from 12 to 72 reversals/sec (rps) in steps of 3 rps or less. To minimize the variability within the noise data, noise values extrapolated from the theoretical function fit to the data were used in the signal-to-noise ratios of AH's spatiotemporal frequency maps (see Figs. 7 and 8A,B).

**Reliability of data**

The data obtained for this paper have a good reliability. The signal-to-noise ratio of the responses was often as high as 40 : 1. The response variability is shown in key conditions in the figures. In this and many other studies we have found that the standard error for a given condition is directly proportional to the response amplitude and has a value of about \(\pm 1.0\) dB (\(\pm 11\%\)). Exceptions to this sometimes occur in the trough between two amplitude peaks, where the standard error may be increased to \(\pm 2.0\) dB.

High intrasession reliability in the shape of the response profile indicated by these low standard errors is also supported by the response stability over time. A very similar profile will be obtained over months and even after a year if the identical stimulation conditions are repeated although the overall response amplitude and signal-to-noise ratio may change. An example of such a replication has been previously reported (Tyler et al. 1978). The fact that slight changes in the stimulus can have a marked effect on the response characteristics makes it necessary to control the stimulus conditions with care in order to obtain such replications. For example, in Fig. 3, a change in spatial frequency
from 1.0 to 1.2 c/deg would reduce the response amplitude by about 60% and eliminate binocular facilitation.

Although intra-observer variability is low, detailed localization of peak responses both in spatial and temporal frequency differ markedly across observers, even though the same electrode placement was always used. The response in each observer is so specific that any attempt to average the results across observers is liable to present a false picture of the individual characteristics, since the specificity across observers is probably a result of the local arrangement of the cortex near the electrode site. We therefore adopted the alternative strategy of taking each observer's results separately, and showing that similar response characteristics may be obtained, although under somewhat different stimulus conditions for each observer.

Procedure

Paid volunteers and laboratory personnel participated in these experiments; data are presented here from 6 observers.

The observers, resting comfortably in a supine position, viewed an overhead mirror image of the 20° × 15° CRT display which appeared at a distance of 37 cm, unless otherwise specified. (Initial studies employed a smaller field size as specified in the figure legends.) Observers were instructed to fixate a central 0.3° star or equal size black spot. For those studies which involved dichoptic stimulus presentations, a circular surround subtending 10° in diameter was placed in front of the rectangular display.

Background EEG activity was monitored continuously to insure observer vigilance during each recording epoch. The slightest EEG distortion, muscle artifact or observer disturbance, was cause for cancellation of the trial and additional readings were then obtained. Recording was continued only when the normal and appropriate baseline noise level was attained.

For discrete recording conditions, a counterphase vertical sinusoidal grating of a given temporal frequency was randomly varied in spatial frequency from trial to trial and presented in a counterbalanced fashion for left eye, right eye or binocular viewing. Such testing was repeated across several temporal frequencies. Binocular and monocular contrast functions for a given spatial and temporal frequency were obtained in a similar fashion except that contrast was varied randomly. Monocular responses were obtained by total occlusion of the fellow eye.

For continuous recording conditions, the same procedures described above (for spatial frequency functions) were followed, except that the counterphase sinusoidal grating was swept in spatial frequency at a slow rate and thus appeared to increase (or decrease) in bar size within the 20 sec recording epoch.

Results and discussion

Binocular interactions and spatial frequency

The binocular and mean monocular visual evoked responses as a function of spatial frequency at 30 reversals per second (rps) for observer DS are plotted in Fig. 2. The upper binocular function shows the typical multiple and narrow spatial frequency tuning function (see Tyler et al. 1978) with peak responses occurring here at approximately 1.7 c/deg and 4.3 c/deg. In normal observers tested in our continuing studies, we rarely find a significant difference in either the amplitude or phase between the right eye (OD) and the left eye (OS) responses (see, e.g., Fig. 5) and we have, therefore, plotted the monocular response as the mean of OD and OS to simplify the data presentation for this figure. Of particular interest is the fact that the prominent low frequency response peak in the binocular function (Fig. 2A) is not present in the monocular function (Fig. 2B). The binocular response in this spatial frequency region appears greater than one might expect from the summed monocular inputs and suggests a limited spatial frequency range where binocular facilitation is thus apparent. At the
higher spatial frequency peak facilitation is absent and, in fact, there is only partial summation. We have previously reported (Apkarian et al. 1977) that in normals the degree of binocular summation may vary between one and at least 5 times the mean monocular response, depending upon the spatial and temporal characteristics of the stimulus.

In order to quantify the degree of binocular interaction we take the sum of the monocular responses and assume that if the response to each eye is generated separately, the binocular response should be the linear sum. This sum is plotted as the dashed line in Fig. 3B and the solid line is the obtained binocular response replotted from Fig. 2A.

In order to clarify the monocular to binocular comparisons, we have plotted the ratio of the binocular to the average monocular responses \(\frac{\text{OU}}{(\text{OD} + \text{OS})/2}\) as a function of spatial frequency in Fig. 3A. It is immediately apparent that great variations occur in the degree of binocular interaction, ranging from zero summation \((\text{B} = \text{M})\) to binocular facilitation \((\text{B} = 3\text{M})\). As is usual in observers with normal vision (see also Amigo et al. 1978; Wanger and Nilsson 1978), no binocular inhibition \((\text{B} < \text{M})\) is seen here.

Because of the high dependence of binocular interactions on spatial frequency, identifying and isolating particular regions of inhibition, summation, or facilitation for clinical or research purposes is cumbersome and time consuming. This drawback can be offset by a technique which can rapidly sample different spatial frequencies such as the continuous recording or sweep technique described in Methods. Binocular interaction data at 28 rps obtained with the spatial frequency sweep are presented in Fig. 4A—E for another observer HS. Each raw trace represents the response to a complete range of spatial frequencies and is obtained in 20 sec. The lower traces give the
Fig. 4. Binocular facilitation for observer HS at 28 rps computed from data presented below. Stimulus field was 20° x 15°, contrast, 0.8. A: binocular to monocular ratio obtained by digitization of the responses in B, D and E. Hatched areas represent facilitation. B: raw binocular response (OU) as a function of spatial frequency. Two separate traces are superimposed to show the repeatability of the responses. Each trace was obtained in 20 sec and represents the continuous analog sweep output. C: computed mean right eye plus mean left eye responses. The monocular responses were digitized and means were obtained for the right eye and left eye responses. The average raw output for 2 sweeps for the right eye (Fig. 4D) and the left eye (Fig. 4E). Directly above is the sum of two mean monocular responses (OD + OS) (Fig. 4C). Fig. 4B shows the raw binocular responses to the same stimulus as the monocular responses. The main features of these results are qualitatively similar to those in Fig. 3 and the ratio of the binocular to the monocular responses shows a range of interactions from zero summation (B = M) to a pronounced binocular facilitation (B > 5M).

Despite the fact that the binocular facilitation is spatial frequency dependent, it should be noted that it does not seem to be associated with particular peaks in the monocular spatial frequency function which occur (for Fig. 4) around 1 c/deg and around 5.0 c/deg. This is consistent with the notion that under binocular stimulation, there is a separate binocular response added to the monocular response, resulting in the appearance of facilitation. In addition, to account for the presence of zero summation in some regions, it is presumed that the monocular responses are in a condition of inhibition or rivalry with each other under binocular stimulation conditions.

Zero binocular summation in normal observers

In general, we find, as do several authors (Campbell and Maffei 1970; Cigánek 1970; White and Bonelli 1970; Harter et al. 1973; Arden et al. 1974), that the binocular response is usually greater than either monocular response, but it is important to realize that there are exceptions to this generalization in normal as well as in abnormal observers. Fig. 5 is presented as one example of zero binocular summation (B = M) in a normal observer over a wide range of spatial frequencies. The topmost plot (Fig. 5A) represents the binocular to monocular ratios from monocular responses were then summed. D: raw right eye (OD) responses as a function of swept spatial frequency. E: raw left eye (OS) responses as a function of swept spatial frequency.
the binocular responses of Fig. 5B and the monocular responses of Fig. 5C. Both the right eye and left eye responses have been included here rather than the mean monocular response to re-emphasize the equality between the two eyes typically obtained with normal observers.

This equality is also seen in the monocular and binocular temporal phase responses (Fig. 5D), and is an important control against the presence of electrical cancellation in the binocular VEP due to temporal phase differences in the responses from the two eyes. If the recorded phase of each monocular response is equal for a given spatial frequency, the responses must add from an electrical standpoint, since electrical subtraction occurs only for phase differences near 180°. In addition, temporal phase can show that subtractive electrical interactions are also not occurring between different neural populations and that the double-peaked nature of spatial frequency tunings is therefore the product of some as yet undetermined type of neural mechanism (Tyler et al. 1978).

Zero summation \( (B = M) \) is present, in this case, across approximately a 3 octave range of spatial frequencies. This lack of summation is then flanked by partial summation \( (B < 2M) \). Facilitation \( (B > 2M) \) is present here, but only for the uniform field flicker response which is plotted on the ordinate at 0 spatial frequency (see Fig. 5, far left). The uniform field flicker response is obtained with a homogeneous field that flickers at the same temporal frequency as the grating modulation (i.e., half the contrast reversal rate). Under this condition, the second harmonic response to uniform field flicker is recorded. The luminance response amplitudes shown here are less than the peak amplitudes of the pattern responses. It is of interest to compare the uniform field flicker and pattern responses with respect to binocular summation. Note that the lower uniform field response suggests that the pattern responses are produced by several pattern-specific mechanisms and are not based on interactions between a single luminance response and a single pattern response (cf., Regan, 1978).

We have found several conditions under which zero summation in a normal observer can occur in the absence of perceived binocu-
lar rivalry. First, zero summation most frequently occurs at trough spatial frequencies as seen here and in Fig. 4. Second, zero summation can occur, although infrequently, within a spatial frequency region not associated with a reduced VEP response (e.g., Figs. 5 and 9). Third, zero summation can occur at low contrast values (e.g., Fig. 6), and fourth, zero summation can occur for uniform field flicker responses, as recently observed in a more detailed investigation of binocularity and contrast modulation (Apkarian and Tyler 1980). It is clear from these results that the binocular response in observers with normal binocular vision is not always greater than the corresponding monocular responses. This fact places severe limitations on the recently described (Fiorentini et al. 1978; Amigo et al. 1978) clinical use of the binocular VEP amplitude as an indicator of or as a screening technique for abnormal binocular vision.

**Binocular interactions and contrast**

Binocular interactions can also vary as a function of contrast. Binocular and mean monocular responses as a function of contrast were obtained at the two binocular peak spatial frequencies of 1.7 c/deg and 4.3 c/deg (Fig. 6, bottom panels) obtained from the spatial frequency tuning curve of Fig. 2A. If perfect summation (B = 2M) is present, the binocular response would equal the linear sum of the monocular responses and thus B/M = 2, as is indicated by the uppermost horizontal line of the top panels. Perfect summation as such is present for the low spatial frequency contrast function (Fig. 6A) predominantly around C = 0.4. Partial summation (M < B < 2M) appears between C = 0.20 to C = 0.30. Facilitation (B > 2M) is most clearly evident for contrast values between C = 0.50 and C = 0.80 with maximum facilitation occurring between C = 0.60 and C = 0.70. It is of interest to note that this contrast function does not saturate. Although saturation is dependent upon several stimulus and recording conditions (Spekreijse et al. 1973; Kulikowski 1977), the lack of saturation at this mean luminance (6.4 cd/m²) and at this low spatial frequency does not conform with previously reported findings.

For the contrast function at the higher spatial frequency (rightmost plot, Fig. 6B), typical saturation as such is again absent. The sharp response attenuation seen at the high contrast values is greater than one might expect from saturation alone and thus has been labeled ‘oversaturation’. Apparent linear summation is also more evident for this contrast function though deviations from B/M = 2 are clearly evident. As with the lower spatial frequency, partial summation occurs most dramatically at lower contrast values.

In general, these results show that the low spatial frequency facilitation of Fig. 6A and the high spatial frequency partial summation
of Fig. 6B for contrast values of approximately 68% (see arrow) are in direct accord with the spatial frequency tuning results obtained at this contrast under the same temporal frequency condition (see Fig. 2). However, these contrast data do not follow the simple linear monocular and binocular relationship of VEP amplitude to log contrast described by Campbell and Maffei (1970), who showed a linear relationship between VEP amplitude and log contrast with monocular and binocular responses of the same observer sharing a common slope. They reported that the binocular response was simply shifted left along the contrast axis by $\sqrt{2}$ in comparison to the monocular function. While it could be argued that the data of Fig. 6A and B could be fit with a straight line over some range of contrast values, the relationship of monocular to binocular responses seen here differs from that described by Campbell and Maffei (1970).

**Binocular interactions and temporal frequency**

Srebro, in a recent article (1978), reported facilitation with binocular responses approximately 30% ($B = 2.6M$) larger than the sum of the monocular responses. This facilitation was obtained at low contrasts ($C < 0.20$) and at a normalized peak temporal frequency. The peak temporal frequency was obtained by averaging the temporal frequency responses across the results of 4 normal observers.

Srebro attributes the facilitation obtained to persistence in uncovering it, as well as to the large number of subjects tested. We agree with the former, but find that a large sample of observers is usually unnecessary when individual response specificity is taken into account.

Although Srebro found facilitation at one normalized peak temporal frequency, we find that binocular interactions, in general, are specific to temporal frequency, as well as to spatial frequency and contrast, and that facilitation, specifically, can occur at a temporal frequency which does not necessarily yield the greatest monocular response. In addition, we find that observers can exhibit dissimilar temporal frequency peak responses. A temporal peak response for one observer can be, for example, the trough for another.

We therefore measured the binocular and monocular spatial frequency tuning as a function of temporal frequency for observer AH. The response amplitudes, obtained under continuous recording conditions (see Methods), were digitized and converted to signal-to-noise ratios. Because of the high resolution and
A wide range of temporal and spatial frequency responses tested (12–72 rps and 0.2–20 c/deg), these data have been presented in the form of spatiotemporal frequency (STF) contour maps (e.g., Fig. 7). The summed monocular (OD + OS) responses are shown in Fig. 8A, the resultant binocular to monocular [OU/((OD + OS)/2)] interactions in Fig. 8B.

The typical features of the VEP as a function of spatial and temporal frequency are evident for both the binocular and monocular STF maps. The narrow temporal frequency tuning observed can show a dramatic response amplitude attenuation with less than a 10% change in temporal frequency. For example, the narrow peak at 48 rps for approximately 4 c/deg drops more than 50% from 48 to 52 rps. (The width of the temporal tuning is actually narrower than it appears due to expansion of the temporal frequency axis by a factor of 4 to facilitate presentation of the data.) In addition to the narrow and multiple temporal frequency tuning, narrow and multiple spatial frequency tuning is also shown.

In the STF maps obtained thus far in our continuing studies, all observers show a tendency toward spatiotemporal reciprocity (Tyler et al. 1978). That is, at higher temporal frequency regions, there is a tendency for the pattern response to shift toward the lower spatial frequencies. Spatiotemporal reciprocity (solid, oblique line) occurs under both binocular (Fig. 7) and monocular (Fig. 8A) conditions.

Fig. 8. A: contour map of the summed monocular spatial and temporal frequency tunings. Details are the same as in Fig. 7, except that equivalent shades of grey represent twice the signal-to-noise ratio (OD + OS). B: contour map of the binocular interactions of Figs. 7 and 8A. Shades of grey represent binocular to monocular ratio values. Hatched areas represent facilitation. For other details, see Fig. 7.
For the monocular STF map (Fig. 8A), a number of peak spatial and temporal frequency responses can be seen throughout, e.g., approximately at 18 rps (3 c/deg), 30 rps (6 c/deg), 38 rps (0.6 c/deg), 42 rps (4 c/deg), 58 rps (1 c/deg). It is important to note that the regions of facilitation (B > 2M) seen in Fig. 8B (hatched regions) generally occur at the temporal and spatial frequencies for which there is a corresponding absence of peak monocular responses. This lack of correspondence between binocular facilitation and monocular peak responses (which was described in two other observers as well, Figs. 3 and 4) further corroborates the notion that binocular mechanisms respond independently of the underlying monocular responses. The 4 most robust and reliable regions of binocular facilitation for this observer occur between approximately 14 and 18 rps at 0.3–0.6 c/deg and between approximately 20 and 34 rps at 0.2–0.6, at 0.4–1.4, and at 1.6–4 c/deg. In the observers tested thus far, facilitation is typically most predominant in the low to medium temporal and lower spatial frequency regions as seen here.

Relationship to stereopsis, fusion and rivalry

As stated previously, we presume that binocular facilitation has some relationship to the mechanism of stereopsis because the binocular response can be greater than the sum of the monocular responses only if there is some kind of facilitatory binocular interaction. This facilitatory interaction could, however, be a property of the binocular fusion system. To test whether binocular facilitation is a property of the stereoscopic system, rather than the binocular fusion system, we expanded the experimental paradigm to 3 conditions of grating orientation: (1) binocular vertical, (2) binocular horizontal, and (3) dichoptic with a horizontal grating to one eye and a vertical grating to the other.

By appropriate spatial and temporal tuning with a counterphase binocular vertical grating stimulus, we obtained, in two different observers, a robust and reliable region of facilitation (Fig. 9) which is a consistent occurrence across a range of adjacent test points within a given stimulus condition. In Fig. 9, the two lower panels depict the summed monocular (dashed lines) and the binocular (solid lines) responses across a spatial frequency range of

Fig. 9. Binocular (solid line, lower panels) and summed monocular (dashed line, lower panels) spatial frequency tunings with vertical gratings for observer CWT (left) at 21.5 rps and for TR (right) at 20 rps. Upper panels depict binocular interaction ratios. Stimulus field was 10° in diameter, contrast, 0.8.

other stimulus conditions are same as in Fig. 9.

Fig. 10. Binocular (solid line, lower panels) and summed monocular (dashed line, lower panels) spatial frequency tunings with horizontal gratings for observer CWT (left) at 21.5 rps and for TR (right) at 20 rps. Upper panels depict binocular interaction ratios. Other stimulus conditions are same as in Fig. 9.
2.3 -- 0 \( U \), Observer CWT

Fig. 11. Binocular (solid line, lower panels) and summed monocular (dashed line, lower panels) spatial frequency tunings under dichoptic stimulus conditions with a vertical grating to one eye and a horizontal to the fellow eye for observer CWT (left) at 21.5 rps and for TR (right) at 20 rps. Upper panels depict binocular interaction ratios. Other stimulus conditions are the same as in Fig. 9.

0.2—20 c/deg. The upper panels depict the binocular interaction ratios. Note the areas of facilitation between 0.3 and 1.3 c/deg for observer CWT (B = 3M) at 21.5 rps and between 1 and 3 c/deg for observer TR (B > 3M) at 20 rps. Although the detailed localization of facilitation in both spatial and temporal frequency differs for each observer, it can be seen (Figs. 10 and 11) that both response profiles change in a similar fashion as a function of stimulus orientation.

It is well known (Hering 1879; Tschermak 1931) and more recently investigated by Westheimer (1978) that stereoscopic depth arises only from horizontal retinal disparities. Westheimer reported that horizontal disparities, whether accompanied by vertical disparities or not, induced the appearance of depth, whereas vertical disparities did not.

In accord with Westheimer’s results is a recent investigation of single units in the cat striate cortex by Von der Heydt et al. (1978). They found that the preferred orientation of disparity sensitive cells was vertical and that disparity cells with horizontal preferred orientation were less frequent. They also found that the dramatic facilitation which they recorded was critically dependent upon disparity. The preferred and optimal vertical orientations, the disparity sensitivity, and the fact that these disparity units responded best to disparities in different parts of the field, led Von der Heydt et al. to conclude that these units serve a stereoscopic function.

A vertical grating stimulus contains discrete horizontal disparities of zero and all multiples of the bar width, whereas a horizontal grating stimulus does not, since a horizontal grating can only contain vertical disparities. If the regions of facilitation seen in Fig. 9 reflect an underlying stereoscopic mechanism, then presenting a binocular horizontal grating stimulus should result in the abolition of the facilitation induced by the binocular vertical grating stimulus. Fig. 10 shows the results of just such a comparison. The facilitation under the binocular vertical grating condition is now reduced under the binocular horizontal grating condition (Fig. 10). In fact, the responses from the previous regions of facilitation are now (within experimental variability) approximately equal to the sum of the monocular responses (B = 2M) as might be expected from a stimulus condition which favors binocular fusion rather than stereopsis.

If it is valid to presume that stimulation with a horizontal grating produces activity in the binocular fusion system (Fig. 10), then a condition of rivalry should disrupt the fusion induced by the horizontal grating stimulus. Rivalry was induced by presenting a vertical grating to one eye and a horizontal grating to the other. Under these conditions, observers reported seeing a rivalry between the horizontal to vertical gratings. This condition of rivalry reduced the binocular summation response to near zero summation (B = M) (Fig. 11). The regions of binocular summation for each observer (Fig. 10) which had previously shown facilitation (Fig. 9) were now roughly equal to the amplitude of a single monocular response (Fig. 11).

Binocular suppression in the absence of
rivalry as discussed previously occurs under the vertical grating condition for observer TR (Fig. 9) in the high spatial frequency region. Zero summation as such is absent for the same area under horizontal viewing conditions (Fig. 10). As a tentative explanation, we would like to suggest that a binocular mechanism stimulated by the vertical grating condition is actively suppressing the separate monocular responses. Note that this mechanism is not present for the horizontal grating condition and, therefore, cannot produce monocular suppression.

Summarizing, despite the complexity of peaks and troughs, acceleration and saturation in both the monocular and binocular responses of the pattern VEP, there are some generalizations that can be made regarding the characteristics of binocularity in the VEP data we have obtained.

1) The types of binocular interactions across our stimulation conditions range from suppression to marked facilitation, although under most stimulation conditions, the binocular VEP shows partial or complete summation with respect to the monocular responses. Thus if one chose a stimulus condition at random, there would be a high probability of obtaining a summation ratio between 1 and 2, which can explain the results of most previous VEP studies. It is important to note that complete summation does not imply the presence of binocular interactions, but would be expected solely from an electrical addition of the responses from two populations of monocular neurons stimulated independently. Partial summation does imply that some type of binocular system is present. If there are binocular neurons in addition to the monocular neurons, as suggested by cortical neurophysiology (Hubel and Wiesel 1963), then partial summation implies the presence of convergence or inhibition between the populations of neurons.

2) Under a small set of stimulus conditions, we find marked binocular facilitation with respect to the monocular responses. This raises the question of whether such facilitation occurs in the same neurons as the monocular responses, or represents the activity of a different set of binocular neurons with different stimulus processing characteristics. We have argued elsewhere that the spatiotemporal response peaks often represent the activity of separable classes of neurons. In the present results, we find that the peaks of binocular facilitation bear no orderly relation to the monocular response peaks. Binocular facilitation peaks can occur at a monocular peak, on its flank, or in regions with no monocular peak. It is therefore probable that the presence of binocular facilitation reflects the activity of a separate set of binocular neurons with different spatiotemporal tuning from the monocular responses. (It is also possible that the same set of cells change their response characteristics under monocular and binocular stimulation, but there is little neurophysiological support for such changing characteristics.) Thus the data are consistent with the hypothesis that the separate responses from monocular and binocular neurons can be distinguished in the scalp VEP.

3) The fine tuning of response characteristics with small changes in spatiotemporal stimulus conditions extends to the domain of stimulus contrast. Not only the response amplitude, but also the degree of binocular summation and facilitation can vary markedly with slight variations in contrast. Furthermore, we find that with increasing contrast, the binocular response usually shows a steeper slope than the monocular response (although there are some clear exceptions). Thus the nature of binocular interactions as a function of contrast depends radically on the other stimulus conditions used in the determination.

4) Regions of binocular facilitation found under a few stimulus conditions occur in the presence of horizontal disparity as would be expected if binocular facilitation were related to stereoscopic processing of horizontal disparities, while other regions do not.

5) The complexity of our data places severe limitations on the use of the VEP for
the assessment of binocularity in patients with disturbances of binocular function, such as strabismic amblyopia. A lack of binocular facilitation or summation for a given stimulus condition may simply reflect the choice of inappropriate stimulus conditions.

Conclusions

This detailed exploration of binocular function using VEP recording techniques suggests that the discrepant reports of binocular interactions in the VEP literature can, in part, be explained by the high degree of VEP specificity to varying stimulus determinants. The stimulus specificity upon which the range of binocular interactions is dependent includes spatial frequency, temporal frequency, contrast and orientation. During the course of this study, these 4 stimulus parameters have been examined in fine detail, but it is probable that other variables, such as luminance, retinal location, electrode placement, field size, and the like are also contributing factors.

Although specificity and narrow tuning of receptive field responses at the single unit level has been known for several years, the information has not been integrated into evoked potential studies. It appears that previous VEP researchers attempting to study binocular interactions have failed to realize the full specificity of macroelectrode recording procedures. The results from this report suggest that fine stimulus tuning techniques may allow recordings from isolated and limited classes of specifically tuned cortical neurons, rather than large broad classes of heterogeneous neural populations. Optimization techniques which rely upon fine tuning procedures here, for example, allowed the identification and study of a high degree of VEP binocular facilitation. These facilitation results, as well as the VEP specificity described here, are more akin to single unit specificity than to previous evoked potential results. It is hoped that the techniques described here will allow the visual evoked potential to serve as a tool for further human electrophysiological investigation of stereopsis, fusion and rivalry, both in normal and in clinical populations.

Summary

The electrophysiology of normal binocular function was investigated by studying the binocular interactions from monocular and binocular visual evoked potentials (VEPs) recorded under a range of stimulus conditions. The amplitude and phase of the steady-state VEPs, which were obtained with sinusoidal gratings temporally modulated in counterphase, were measured with synchronous narrow-band filtering techniques. Binocular interactions were investigated as functions of spatial frequency, temporal frequency and contrast. Detailed sampling and testing within each stimulus domain revealed an unprecedented degree of VEP specificity in the extent of binocular interaction, which varied from zero summation to pronounced facilitation.

Binocular facilitation was explored in terms of its relation to the neural mechanisms subserving binocular function. VEP correlates of rivalry, fusion and stereopsis were obtained.

The facilitatory binocular interactions, revealed by careful spatial and temporal stimulus manipulations, were akin more to the neurophysiological responses of single neurons than to previously reported evoked potential work. The relationship between the specificity and narrow tuning of the binocular interactions recorded with VEP techniques and those recorded with single unit techniques is discussed.

Résumé

Binocularité dans le potentiel évoqué visuel chez l'homme: facilitation, sommation et suppression

On a cherché à cerner l'électrophysiologie de la fonction binoculaire normale par l'étude
des interactions binoculaires entre potentiels évoqués visuels (PEV) mono- et binoculaires enregistrés dans une gamme de conditions de stimulation. L’amplitude et la phase des PEV en régime stable, obtenus avec des réseaux sinusoidaux temporellement modulés en opposition de phase, furent mesurées avec des techniques de filtres synchrones à bande étroite. Les interactions binoculaires furent étudiées en tant que fonctions de la fréquence spatiale, de la fréquence temporelle et du contraste. En effectuant des échantillonnages et des tests précis, pour chaque domaine de stimulation, on a pu noter un degré sans précédent de spécificité des PEV dans l’étendue des interactions binoculaires, lesquelles varient d’une sommation nulle à une facilitation prononcée.

La facilitation binoculaire a été explorée en termes de sa relation avec les mécanismes neuronaux qui sous-tendent la fonction binoculaire. Des corrélations entre PEV ont été obtenues pour le conflit, la fusion et la stéréopsis.

Les interactions binoculaires facilitatrices révélées par des manipulations fines du stimulus spatial et temporel se sont montrées plus proches des données sur les réponses unitaires des unités isolées qu’à celles précédentes sur les potentiels évoqués. On discute des relations entre la spécificité et l’accord étroit des interactions binoculaires enregistrées avec les techniques de PEV et ceux enregistrés avec les techniques unitaires.

References


Apkarian, P. and Tyler, C.W. Effects of modulation depth and binocularity in the pattern evoked potential. 0, submitted.


Nakayama, K., Apkarian, P. and Tyler, C.W. Human visual evoked potentials: isolation of cortical populations narrowly tuned to spatial frequency. In: E. Donchin (Ed.), Neurophysiology and Psychol-
Perry, N.W., Childers, D.G. and McCoy, J.G. Binocular
addition of the visual evoked response at dif-
ferent cortical locations. Vision Res., 1968, 8:
567—573.
Pettigrew, J.D., Nikara, T. and Bishop, P.O. Binocular
interaction on single units in cat striate cortex:
simultaneous stimulation by single moving slit
with receptive fields in correspondence. Exp. Brain
Poggio, G.F. and Fischer, B. Binocular interaction
and depth sensitivity in striate and prestriate cor-
text of behaving rhesus monkey. J. Neurophysiol.,
Regan, D. Assessment of visual acuity by evoked po-
tential recording: ambiguity caused by temporal
dependence of spatial frequency selectivity. Vision
Spekreijse, H., Van der Tweel, L.H. and Zuidema, Th.
Srebro, R. The visually evoked response: binocular
facilitation and failure when binocular vision is
Tschermak, A. v. Optischer Raumsinn. In: A. Bethe
et al. (Eds.), Handbuch der Normalen und Patho-
logischen Physiologie, Vol. 12, Pt. 2. Springer, Ber-
lin, 1931: 929.
Tyler, C.W., Apkarian, P. and Nakayama, K. Multiple
spatial-frequency tuning of electrical responses
from human visual cortex. Exp. Brain Res.,
Tyler, C.W., Apkarian, P., Levi, D.M. and Nakayama,
K. Rapid assessment of visual function: an elec-
tronic sweep technique for the pattern VEP.
Von der Heydt, R., Adorjani, Cs., Hanny, P. and
Baumgartner, G. Disparity sensitivity and receptive
field incongruity of units in the cat striate cortex.
Wanger, P. and Nilsson, B. Visual evoked responses to
pattern-reversal stimulation in patients with am-
blyopia and/or defective binocular functions. Acta
Westheimer, G. Vertical disparity detection: is there
an induced size effect? Invest. Ophthal., 1978, 17:
545—551.
White, C.T. and Bonelli, L. Binocular summation in
the evoked potential as a function of image qual-