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STEADY STATE VISUAL EVOKED POTENTIALS IN THE ALERT PRIMATE

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Abstract—Macaque monkeys were trained to fixate a small spot while we recorded epidural steady state visual evoked potentials (SSVEP) in response to counterphase modulated sinusoidal gratings. This led to the following results: (1) the SSVEP can show either broad or narrow spatial frequency tuning, depending on electrode location, temporal frequency, contrast and method of analysis. (2) The SSVEP can also show narrow temporal frequency tuning, as narrow as 0.5 octave at half height. (3) Contrast functions relating VEP amplitude to log contrast were highly nonlinear. We propose that they are the composite of at least two distinct linear functions, one with a shallow slope for low contrasts and one with a significantly steeper slope for the higher contrasts. (4) Extrapolation of the low contrast function to zero voltage can lead to an excellent match with psychophysical functions. A similar extrapolation of the high contrast function, however, leads to a contrast value much higher than the psychophysical threshold. These findings suggest that the SSVEP can reflect the activity of two distinct neural mechanisms responsive to pattern stimulation. The degree to which either mechanism is evident determines the spatial and temporal frequency tuning of the VEP.

INTRODUCTION

As part of a long range plan to examine an appropriate animal model for human visual evoked potentials (VEP) we have chosen an alert old world primate, *Macaca fasicularis*. We made this choice for several reasons.

First, there is a wealth of psychophysical evidence to suggest that the macaque visual system is very similar to that of man. Detailed features of the spatial contrast sensitivity (De Valois *et al.*, 1974a), color (De Valois *et al.*, 1974b), binocular disparity (Harwerth and Boltz, 1979), and flicker (Merigan, 1980) show these monkeys to be almost identical to the human, much closer, for example, than the cat (Berkeley, 1978). Moreover, in a preliminary study we have investigated the steady state pattern VEP in the monkey (Nakayama *et al.*, 1980) and found many similarities with findings obtained in humans. Some aspects of these findings were recently confirmed by van der Marel *et al.* (1981) on the basis of transient VEP recordings.

A second important advantage is that the monkey visual cortex is the object of much attention using a wide variety of physiological and anatomical techniques (Schiller *et al.*, 1976; Zeki, 1978; Van Essen, 1979; Lund, 1981). With this background information, correlations between human and monkey VEP could lead to the establishment of the long sought-after identification of some human VEP components in terms of basic physiological processes and anatomical structures.

We begin with the steady state VEP (SSVEP) mainly because it has received wide attention with humans and no comparable attention in the alert primate. Of particular interest to us are two prominent human SSVEP results.

First are the pioneering experiments of Campbell and Maffei (1970) correlating the VEP to the psychophysical characteristics of pattern sensitivity. They established that the relation between log contrast and VEP amplitude is linear. They also extrapolated this linear function to zero microvolts and found a close correspondence between the extrapolated contrast value at zero signal and the psychophysical threshold. Thus, the reciprocal of VEP threshold contrast closely matched the psychophysical contrast sensitivity function. The curve is broadly tuned and unimodal.

Second is a recent finding appearing contrary to that obtained by Campbell and Maffei: the discovery that the human VEP amplitude can be very narrowly tuned with respect to spatial frequency (Tyler *et al.*, 1978). Instead of a broad curve when plotting VEP amplitude vs spatial frequency, there was an extreme sensitivity to small changes in spatial frequency and the characteristics of spatial frequency tuning varied with temporal frequency (see also Regan, 1978). The tuning functions could have two or even three very narrow peaks (Tyler *et al.*, 1978, 1979), each as narrow as those seen for individual cortical neurons (Schiller *et al.*, 1976). Furthermore, in some cases extrapolation of the amplitude vs log contrast curve fails to predict the psychophysical threshold (Apkarian and Tyler, 1982). These latter results are in partial conflict with the findings of Campbell and Maffei, despite the similarity of experimental conditions and method of analysis.

In this paper we outline some general features of the steady state pattern VEP in the alert monkey,

noting the degree to which they conform to the characteristics of the human VEP described above.

METHODS

Visual stimulation

Vertical sinusoidal gratings modulated in counterphase were generated on the face of a cathode ray oscilloscope (Hewlett and Packard, model 1332A). The luminance (L) of any point on the screen was a sinusoidal function of its horizontal position (x) and a sinusoidal function of time (t).

$$L(x,t) = A \sin(2\pi f_t t) \sin(2\pi f_s x) + L_0 \qquad (1)$$

where f_t is the temporal frequency and f_s is the spatial frequency of the luminance modulation and L_0 is the mean luminance. Contrast ($100\% \times A/L_0$) could be experimentally varied so that it ranged between 1 and 83%. Linearity was maintained over this large contrast range by careful compensation of the non-linear phosphor characteristics of the monitor oscilloscope using a tunable 8-element resistive diode network. Unless noted, the stimulus field subtended an angle of 7.3° (horizontal) × 5.3° (vertical) and was presented to the contralateral hemifield. The monkey fixated a red LED of 4 min arc diameter, placed 24 min arc away from the edge of the stimulus field (see Fig. 2). Viewing distance was set at 83 cm.

Electrical recording

Because the SSVEP in response to counterphase modulated gratings is roughly sinusoidal at the second harmonic, especially for high rates of stimulation (Campbell and Maffei, 1970), we employed a narrow band filter tuned to this harmonic to maximize the signal-to-noise ratio. Because the counterphase reversal rate is twice the modulation rate (f_t), as defined in equation 1, this is equivalent to centering our filter at the first harmonic of the counterphase reversal frequency, which we call "recording frequency". In practice, we derived the amplitude and phase of this second harmonic component (Regan, 1972) by performing a sine and cosine multiplication at the counterphase frequency with EEG signal.

Electrical signals from the cortical surface were amplified by a wide band high impedance preamplifier ($10^{12}\ \Omega$) having a flat frequency response from d.c. to 10 KHz. Following this amplification, the brain potentials were passed through a first order low pass filter having a cut-off frequency (−3 dB) of 480 Hz. The phase lag of a 1st order low pass filter is given by $\phi = \tan^{-1}(f/f_c)$, where f is the frequency at which the phase is measured and f_c is the cut-off frequency. Because this cut-off frequency is over 10-times higher than our highest recording frequencies (see below), the maximum phase lag introduced by our electronic apparatus is 5°. This amounts to a less than 1% error in the measurement of phase change over the temporal frequencies tested (as in Fig. 4).

Preparation of the monkeys

Surgical procedures were performed on two adult male Java monkeys (*Macaca fascicularis*). Under a combination of Nembutal and Ketamine anesthesia, chronically implanted cortical EEG and EOG electrodes were secured. They consisted of Ag–AgCl pellets (In Vivo Metrics Systems, Healdsburg, CA) implanted in the outer canthi of the orbits and between the eyes for DC-EOG recordings, and in the skull over the occipital cortex for the VEP recordings. Six epidural electrodes were secured in the bone along a line corresponding to the visual field below the horizontal meridian, ranging from the fovea to approximately 10° into the contralateral fields (Zeki, 1978). The reference electrode for all recordings was placed on the midline over the frontal lobe, approximately 20 mm posterior to the supraorbital ridge.

For head restraint, we made a custom face/head frame, consisting of two adjustable half-shells moulded from dental impression compound.

Electrode localization

At this point we have sacrificed only one of the two monkeys. The position of the electrodes relative to the surface of the brain of monkey No. 1 was determined by a post mortem examination. We found that 5 out of 6 electrodes lay posterior to the lunate sulcus over the occipital lobe (see Fig. 2). Thus, they were located over the striate cortex (V1), placed along a line, which extends downward and outward into the contralateral hemifield (Zeki, 1978). The 6th electrode was located over a pre-lunate region, possibly corresponding to V4 (see electrode No. 6 in Fig. 2).

Training of fixation

To ensure a repeatable visual stimulation on a given part of the retina and to guarantee that the monkeys were indeed alert, we trained them to maintain fixation according to a technique developed by Eckmiller and Mackenben (1978). The training consisted of two stages: first they were trained in their home cages to press a bar upon brightening of a fixation light. During the second more rigorous laboratory phase the size and brightening of the fixation light were gradually reduced. Correct responses were rewarded by small amounts of water. Except for one day per week, the monkeys had to earn their entire daily liquid intake this way. Both phases of training were completely automated and controlled by a microcomputer (Commodore PET 2001). During the experimental phase, the monkeys made 300–800 correct responses per day.

Experimental procedure

The daily experimental routine consisted of a series of runs, each of which was a complete measurement of a particular visual function. With a given run we measured the amplitude and phase of the SSVEP as a function of one out of several possible variables,

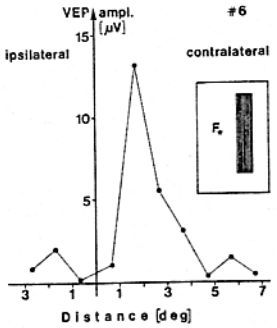

Fig. 1. Amplitude of the steady state visual evoked response as a function of the monkey's fixation position relative to a 1° × 5° vertical slit containing a counterphase-flickered vertical grating. Spatial frequency of the grating was 10.3 c/deg, reversal rate, and thus "recording frequency" (see Methods), was 16 Hz, and the contrast set at 35%. The abscissa shows horizontal retinal eccentricity of the visual stimulus expressed as distance of the fixation light (F) from the middle of the slit (see inset). The distance, at which the response was maximal, was 1.6°. Recordings were made from monkey No. 1 at electrode No. 6 (for localization see Fig. 2).

either temporal frequency, spatial frequency, contrast, or retinal locus. For example, to measure the influence of spatial frequency, it alone was varied, leaving the other parameters constant. The order of presentation of different spatial frequencies was randomized throughout the run.

Six sets of data (amplitude and phase) were obtained at each of 10–13 variable values, so that each run consisted of 60–78 (typically 72) trials. Between 4 and 10 complete runs were recorded per day. The results from all data sets corresponding to the same variable value were added vectorially. Thus, the sine and cosine components of the sinusoidal signal were separately averaged. This was followed by calculation of amplitude $A = (x^2 + y^2)^{1/2}$ and phase $\phi = \tan^{-1}(y/x)$, where x and y are the mean of the cosine and sine components, respectively. Variability of the amplitude and phase was calculated by separately computing the amplitude and phase of the signal on each trial and then calculating the standard error for the block of six trials.

The ongoing EEG and EOG was continuously presented on a monitor oscilloscope and closely observed throughout the recording sessions. The experimenter manually initiated a 3 sec epoch of stimulation and recording when the monkey was calm and attending to the fixation light. This was determined on the basis of the EOG and EEG traces, as well as by the performance level of the monkey in the trained paradigm. The actual recording period was signalled to the experimenter by a LED next to the oscilloscope displaying the EOG and EEG. Thus, trials containing EEG artifacts or eye fixation lapses could be easily discriminated and excluded from the data analysis. The particular variable value associated with the rejected data was automatically interspersed later in the series by the computer.

By reducing spurious responses, the rejection technique allowed us to achieve excellent reliability and reproducibility of the experimental data. In both monkeys, the standard error of amplitude means for each variable value within a run ranged from 4 to 30% of the mean (typically it was 10%), showing an inverse correlation with signal amplitude. Specifically, at amplitudes above 10 μV, the mean variability of standard errors was 11.4% and 8.4%, while at values below 10 μV it was 20.6% and 12.9% for monkey Nos 1 and 2, respectively. Amplitude values below 10 μV were generally regarded cautiously and were included in the data evaluation (such as the estimation of contrast function slopes, see below) only if the corresponding phase values showed a standard error of less than 12°. In cases when runs with a particular set of parameters were repeated, the maximal variability (standard error) between runs was 12% of the mean.

RESULTS

Retinal localization

Before describing the main results, it is best to give some indication as to the area of the visual field that can elicit a VEP, also providing evidence for the accuracy of fixation during the stimulus presentation. We varied the horizontal position of the fixation LED relative to a 1 × 5° vertical slit, within which the grating could be seen. The response amplitude was measured as it varied with retinal location. Figure 1 shows the amplitude of visual evoked potential as a function of the horizontal position of the slit.

Several conclusions can be drawn from the shape of this sharply peaked function. First, it can be assumed that the portion of the visual field, which contributes to the VEP recorded by this particular electrode (No. 6), must be relatively circumscribed, not exceeding 3° in horizontal extent. Second is the conclusion that undesired eye movements must also be correspondingly small, otherwise the response would be smeared out to a much greater degree than that shown in Fig. 1. A comparable degree of spatial specificity was recorded when we changed the vertical position of a horizontal slit. Thus, the results provide an important validation of our training technique to maintain fixation. Finally, there is no response from the ipsilateral visual field, a very different result from what is reported in the human (Blumhardt and Halliday, 1979).

Spatial frequency tuning

The systematic studies began with an examination of the spatial frequency tuning of the pattern visual evoked potential. As mentioned earlier, two types of VEP findings in humans are relevant. First is the broad curve relating VEP contrast sensitivity and spatial frequency derived by extrapolating contrast functions to zero amplitude (Campbell and Maffei, 1970). Second are the surprisingly narrowly tuned

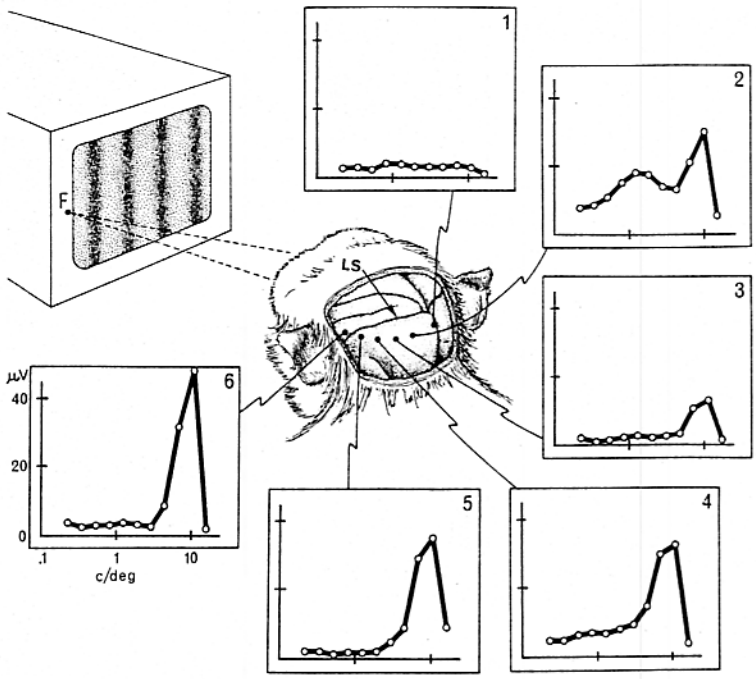

Fig. 2. Spatial frequency tuning in the VEP of monkey No. 1. Each curve represents a spatial frequency characteristic at the electrode location which was reconstructed post mortem. The electrodes were arranged along a horizontal line, the distance between Nos 1 and 6 was 30 mm. Numbers 1–5 were located over the striate cortex, whereas No. 6 was over a pre-striate area as can be determined to its position to the luneate sulcus (LS). The foveal representation was probably slightly below electrode No. 5. Each data point constitutes the average of 24 values, taken from 4 complete functions (6 repetitions per variable value), which were recorded on different days. Each one of the single functions showed all qualitative features displayed in the average curves. The scaling of the labeled axis of the lower left function (No. 6) is valid for all 6 curves. Contrast was 30%, mean luminance was 20 cd/m^2, and reversal frequency was 16 Hz.

spatial frequency functions for fixed contrasts (Tyler *et al.*, 1978).

Plotting monkey VEP amplitude as a function of spatial frequency revealed extremely narrow spatial frequency tuning. Figure 2 shows the response of 6 different electrodes to counterphase-modulated gratings at different spatial frequencies, including the localization of each electrode relative to the convolutions of the occipital region of the brain. We found a prominent, narrowly tuned spatial frequency peak for at least 4 locations. What is surprising is that, with the exception of one electrode (No. 2), this monkey showed essentially no response over the wide range of spatial frequencies between 0.2 and 2 c/deg, a range of spatial frequencies which must be clearly visible to the monkey (DeValois *et al.*, 1974a).

While these results confirm earlier findings seen in man (Tyler *et al.*, 1978), it should be noted that more broadly tuned functions could also be obtained, depending on temporal frequency. Figure 3 shows spatial frequency tuning in the second monkey at electrode No. 3 (located as shown in Fig. 2) for 5 temporal frequencies. Note the moderately broad tuning for the lower spatial and temporal frequencies, and also the existence of a narrow high spatial frequency peak at almost all temporal frequencies. Thus, as in the human, the spatial frequency tuning functions are highly dependent on temporal frequency. This confirmed our earlier findings in monkey No. 1 (Nakayama *et al.*, 1980).

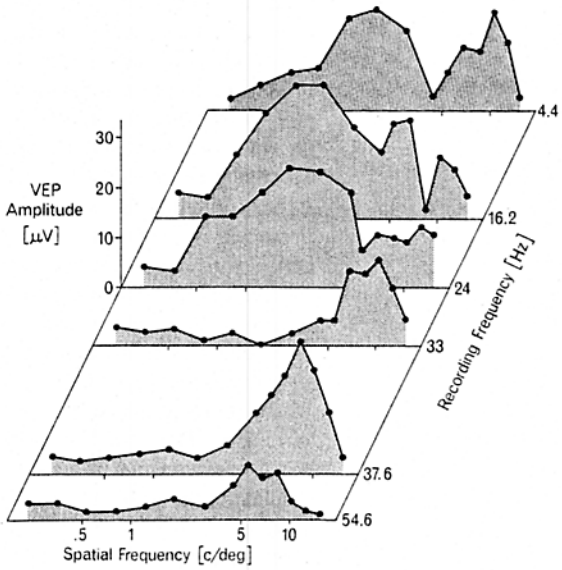

Fig. 3. Spatial frequency tuning functions obtained at different recording frequencies in electrode No. 3 (monkey No. 2). Multiple spatial frequency peaks are only seen at lower recording frequencies (4.4–24 Hz).

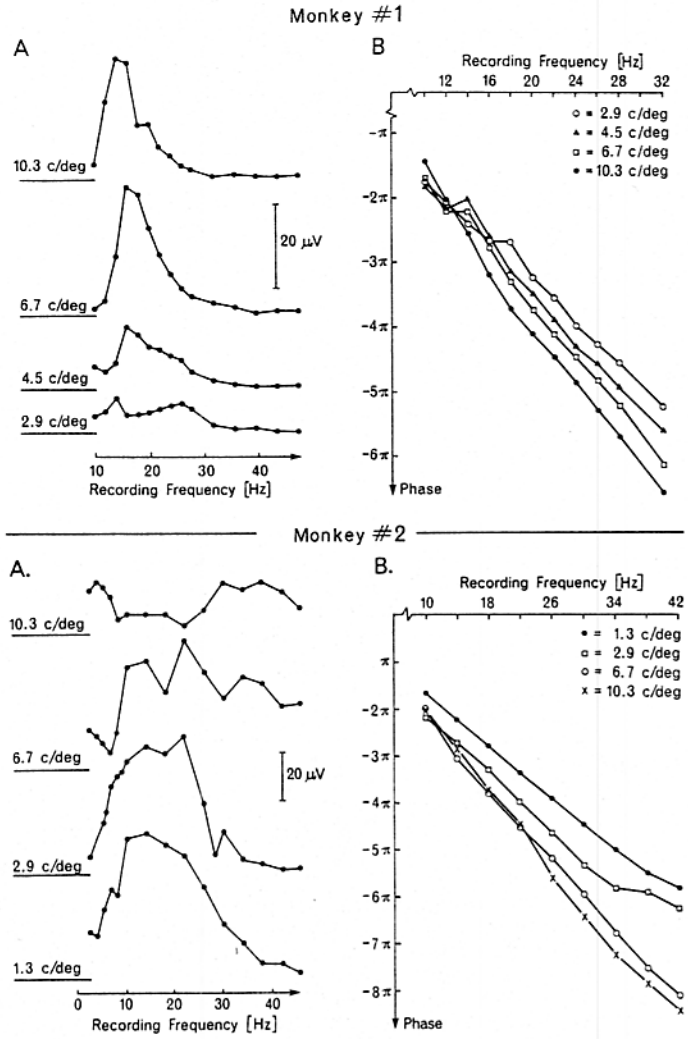

Fig. 4. Temporal frequency characteristics in monkey No. 1 (electrode No. 5) and monkey No. 2 (electrode No. 3). Curves on the left (A) represent VEP amplitude vs temporal frequency for 4 selected spatial frequencies. The baseline of zero response for each function is represented by the solid line to the left of each function. Note the very narrow temporal frequency tuning in monkey No. 1 for the higher spatial frequency gratings. Functions on the right side (B) show the phase lag vs temporal frequency for the same set of spatial frequencies. Note that the phase lag for higher spatial frequencies is greater in both monkeys.

Temporal frequency tuning

In addition to the spatial frequency tuning, we systematically investigated the response to different temporal frequencies in each monkey. Figure 4A shows the results at four representative spatial frequencies in each monkey. Note the very sharp temporal tuning in monkey No. 1 and its dependence on spatial frequency. Monkey No. 2, at a different electrode, showed less pronounced temporal tuning. A second feature to be noted in both monkeys is the systematic change in recorded phase as temporal frequency is increased (see right hand portion of Fig. 4). Phase lag increases with increasing temporal frequency, and from the separation of the curves corresponding to different spatial frequencies it should be clear that this increasing phase lag is more pronounced for higher spatial frequencies. If one interprets the slope of these phase lag vs temporal frequency curves as representing a simple delay in the afferent pathway (Regan, 1972), the results tally with human results showing increasing sluggishness of higher spatial frequency mechanisms (Breitmeyer, 1975; Parker and Salzen, 1977; Williamson *et al.*, 1978). For example, the equivalent latencies at 2.9 and 16 c/deg seen in monkey No. 1 are 86 and 101 msec, respectively. This was computed by the formula $\Delta t = \Delta f/2\pi\Delta\phi$, where Δt is the latency, Δf the difference in frequency and $\Delta\phi$ the difference in recorded phase.

Contrast

Before providing some comment on the significance of the temporal and spatial frequency tuning charac-

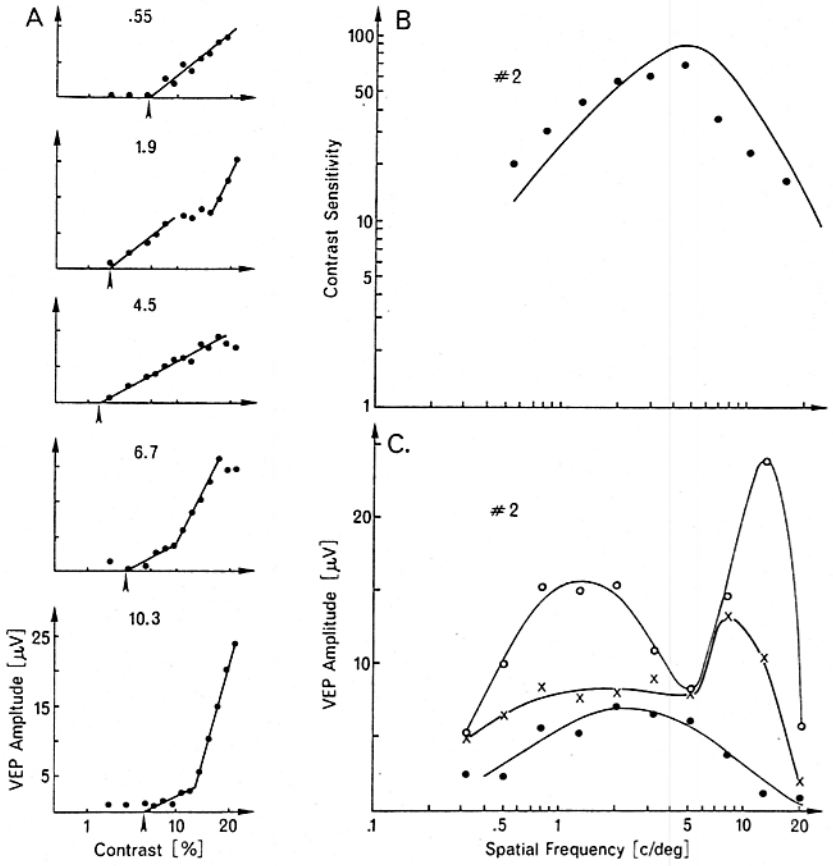

Fig. 5. (A) VEP amplitude plotted as a function of log contrast for 5 different spatial frequencies (represented by the number above each contrast function). Note the existence of piecewise linear contrast functions. Arrows along the abscissa denote the x-intercept of the lower limb of this function, defined as the extrapolated VEP threshold. (B) The solid line is the contrast sensitivity function obtained behaviorally by DeValois *et al.* (1974a) at a comparable luminance level. Solid dots represent the VEP contrast senstivity (reciprocal of VEP threshold obtained from contrast functions) in (A). Note the close correspondence between VEP and psychophysical contrast sensitivity, both on a relative and an absolute scale. (C) VEP amplitude vs spatial frequency for 3 levels of contrast (dots = 9%, ×'s = 18%, open circles = 32%). Note that narrow spatial frequency tuning is evident at intermediate and prominent at the highest contrast values. All data in this figure taken from monkey No. 1, electrode No. 2 (as seen in Fig. 2). Recording frequency was 16 Hz.

teristics, it is best to consider how the evoked potential varies with stimulus contrast or modulation depth, thus following the approach used by Campbell and Maffei (1970). Generally, it has been found that in most VEP work the response amplitude rises as a function of modulation depth and then saturates, giving rise to a decelerating non-linear function (Spekreijse, 1966). With respect to the pattern evoked potential, Campbell and Maffei (1970) have shown that VEP amplitude rises linearly with log contrast to the stimulus modulation and this has been validated over a range of contrasts even very close to threshold (Campbell and Kulikowski, 1972). As mentioned earlier, Campbell and Maffei (1970) also found that the x-intercept of this linear function predicts the psychophysical threshold.

In our human laboratory, we have often seen a mismatch between extrapolated VEP threshold and the psychophysical threshold, with the VEP threshold as much as ten times higher than the psychophysical threshold (Apkarian and Tyler, 1981). Thus, it seemed especially important to explore the variations of VEP threshold with contrast in the monkey as well. To examine this influence, over 130 contrast functions were obtained from both monkeys, covering a wide range of spatial and temporal frequencies at several electrode locations.

The slopes of the contrast functions were determined graphically. In the amplitude range close to the noise level, data points used for the projection of the best-fitting line were selected on the basis of amplitude and phase variation. Only those data points with phase standard errors of less than 12° were regarded as clearly distinguishable from noise. The best-fitting linear function was extrapolated to zero microvolts and the corresponding contrast was taken as the threshold.

In Fig. 5A we show representative log contrast vs VEP amplitude functions in monkey No. 1, obtained at different spatial frequencies. These functions very

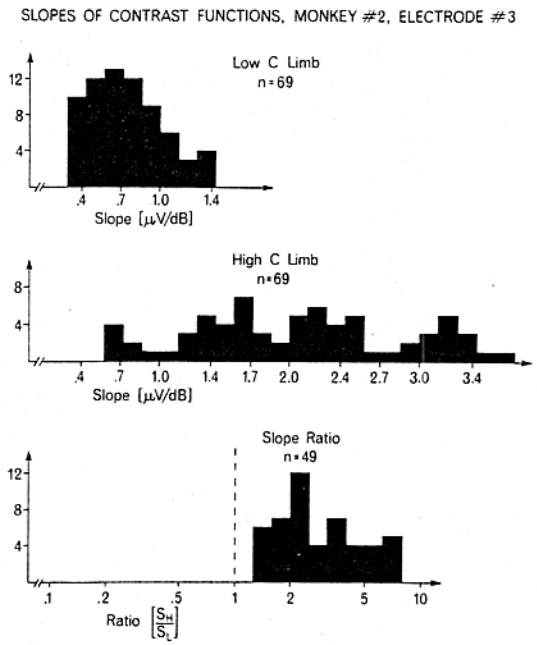

Fig. 6. Slopes of the high and low contrast limb of 87 contrast functions measure in monkey No. 2 (electrode No. 3). (A) Histograms showing the distribution of slopes of the low contrast limb. (B) Histogram showing the distribution of slopes of the high contrast limb. (C) Histogram showing the ratio of slopes of high/low contrast limbs. If slopes were identical at low and high contrast, this bottom histogram should be centered around 1.

often consisted of two rising linear segments, or "limbs". Either one of the limbs could saturate independently. The slope of the rising function was always shallower at low contrasts and steeper at high contrasts. The steepness of the high contrast function should be emphasized. For example, in the bottom curve in Fig. 5A (corresponding to a spatial frequency of 10.3 c/deg), a simple doubling of contrast from 11.5% to 23% leads to a five-fold increase in the VEP amplitude.

Although the existence of a low and high contrast function is clearly visible in the data presented in Fig. 5A, an even more systematic picture of this difference emerges by comparing the slopes for all 87 contrast functions measured in monkey No. 2 (electrode No. 3). To make this comparison, we defined any straight function having an extrapolated x-intercept of 5% or less as the low contrast limb. Conversely, any function with an extrapolated intercept above 5% contrast was defined as the high contrast limb. The histograms in Fig. 6A and B shows the distribution of slopes for all high and low contrast functions obtained from monkey No. 2 at electrode No. 3. It should be clear from this comparison that the two distributions are very different.

The low contrast function has a mean slope of about 0.7 microvolts/dB of contrast, whereas the mean slope of the high contrast function is approximately 3 times as great (mean = 2.0 μV/dB). Considerable variability in the slope of the high contrast function should be noted, however. Of the 87 contrast functions measured in monkey No. 2, 49 (56%) contained two distinct linear limbs. A histogram of the ratio of the two slopes for these cases is seen in Fig. 6C. If the slopes of the high and low contrast portions were the same, the histogram would be expected to be centered around a ratio of 1. This is clearly not the case. The distribution is highly skewed towards a ratio much greater than 1, showing a mean ratio of 2.8. Systematic analysis of a lesser number of contrast functions in monkey No. 1 (N = 37) showed an even more pronounced slope ratio (mean ratio = 5.0).

In both our monkeys, the presence of two limbs in the contrast function did not vary systematically with spatial frequency. It was found, however, that temporal frequency was of much greater influence in this respect. This was not investigated in monkey No. 1, but in monkey No. 2 contrast functions were obtained at a wide range of recording frequencies (between 5.8 and 50.0 Hz). The lowest and highest frequencies, at which two rising limbs could be seen, were 5.8 and 26 Hz, respectively. Most of the functions (56) were recorded at 11 or 16.8 Hz. Within this group, the percentage of two-limbed curves was even higher than stated above (45 out of 56 = 80%).

Having explored the influence of contrast over a wide range of spatial and temporal frequencies as well as electrode locations, it is possible to make a direct comparison with the results obtained by Campbell and Maffei (1970). To do this, we chose the low contrast limb of the contrast function and noted the contrast at which this function extrapolates to zero amplitude. The arrows in Fig. 5A show the position of this extrapolated VEP thresholds. Moreover, the reciprocals of the thresholds (the sensitivity) as a function of spatial frequency are shown as dots in Fig. 5B. The solid line in the same figure shows the behaviorally determined contrast sensitivity function in the same species under comparable luminance conditions (DeValois *et al.*, 1974). It is evident that the extrapolated VEP data provide a good fit to psychophysics.

In some instances, however, the low contrast limb of the function was either absent or indistinct. This was often the case for electrode No. 6 of monkey No. 1 (see Fig. 7A). In these cases, only the high contrast limb is sufficiently defined to be extrapolated. Not surprisingly, the resulting contrast sensitivity curve falls far short of the psychophysical curve (see Fig. 7B). What remains is a reduced sensitivity over a very limited range of spatial frequencies. The presence of a low contrast limb in the contrast function is therefore decisive in determining whether the VEP results conform to the psychophysics. The question whether a low contrast limb can be seen, is dependent on several factors. One of them is electrode location, as seen in the example above.

Another determining factor is temporal frequency. In Fig. 8 we see two extrapolated VEP contrast sensitivity curves for monkey No. 2, obtained at 11 and 17 Hz. At the lower recording frequency (11 Hz), the

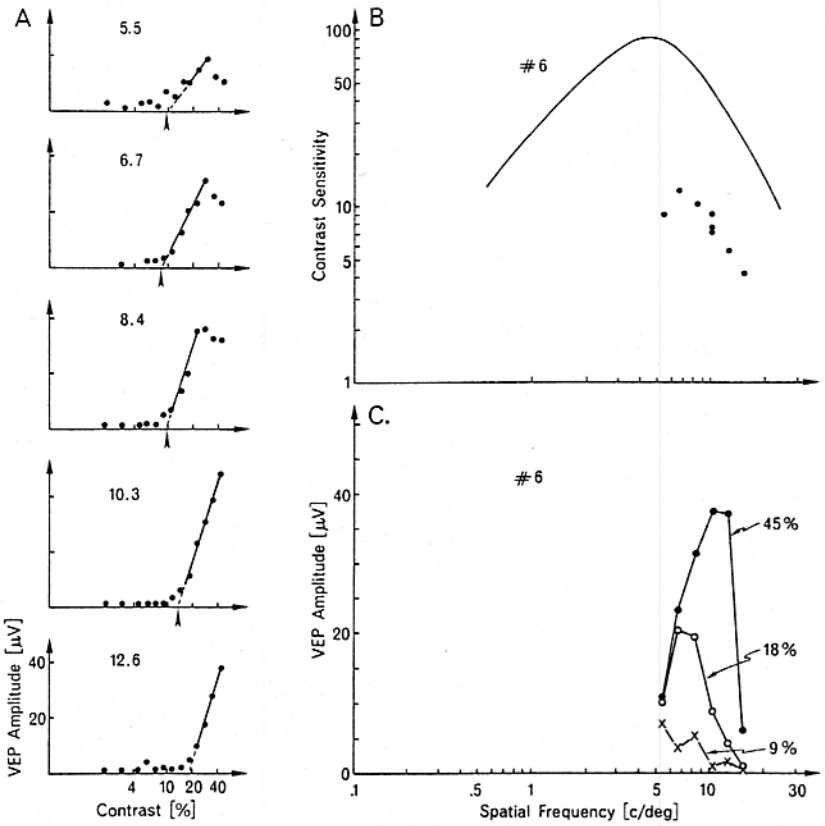

Fig. 7. (A) VEP amplitude vs log contrast for 5 spatial frequencies. (B) Mismatch of extrapolated VEP thresholds and psychophysics in monkey No. 1 (same as in Fig. 5), but at a different electrode site (No. 6). The low contrast limb was difficult to discern in most of the functions [see (A)], so that the extrapolation was performed on the high contrast limbs. The result is a reduced contrast sensitivity curve, confined to higher spatial frequencies (dots). (C) Amplitude vs spatial frequency for 3 different contrasts. These data were extracted from runs with contrast as variable. Note that this does not cause emerging of broader spatial frequency tuning at lower contrasts, as compared to Fig. 5A). This is a direct consequence of the very reduced or absent low contrast response at any spatial frequency for this electrode.

extrapolated thresholds were unusually high for intermediate spatial frequencies, and as a consequence the extrapolated VEP contrast sensitivity function shows a reduced sensitivity notch around 5 c/deg (Fig. 8B). On the other hand, a good match is obtainable at the higher frequency of 17 Hz (Fig. 8A).

DISCUSSION

Comparison of monkey and human results

Three similarities between monkey VEP results and those obtained in humans should be noted. First is the existence of narrow spatial and temporal frequency tuning. This joint dependence has been seen in humans under a wide variety of conditions (Tyler *et al.*, 1978). In both, monkey and man, the tuning is usually very pronounced and reproducible but hard to predict in specific details for a given subject/animal. At any electrode location, a set of spatial and temporal frequency peaks will be constant over months or even years, but at the same location (in skull coordinates) different sets can be recorded from different subjects/animals.

Second is the existence of multi-limbed linear functions when plotting monkey VEP amplitude vs log contrast, which has been reported for humans by Campbell and Maffei (1970) and Apkarian and Tyler (1981).

Finally, there can be the same match between the extrapolated monkey VEP thresholds and psychophysics as in the human (Campbell and Maffei, 1970).

The only notable difference between the two species lies in the topographical distribution of the responses, namely that the macular responses of the monkey are confined to the contralateral cortex whereas in man this is less clear. In fact a seemingly paradoxical larger response in the human ipsilateral hemisphere can occur (Blumhardt and Halliday, 1979). This latter difference is not surprising, however, given the large difference in the topographic layout of the visual cortex in man and monkey. In man, the left and right hemirepresentations of the macular region on the primary visual cortices are very close together and somewhat distant from the recording site. Thus, the orientation rather than the position of the dipole generators with respect to the recording electrode is most critical

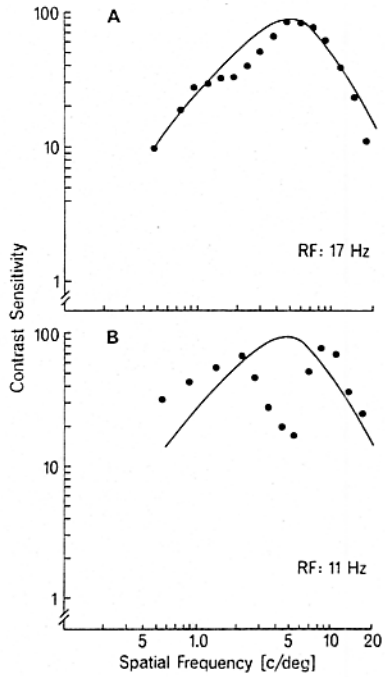

Fig. 8. (A) Good match of extrapolated VEP threshold and psychophysical threshold in monkey No. 2 (electrode No. 3) at 17 Hz recording frequency (RF). (B) Mismatch of extrapolated VEP threshold and psychophysics in the same monkey and the same electrode, but at a different recording frequency (11 Hz).

(Blumhardt and Halliday, 1979). In the monkey, however, the representations of the macular region on the striate cortex are very far apart and on the surface of the brain. As a consequence, the response of each hemifield is very well localized to the expected contralateral side. This leads us to assume that the demonstrated similarities of VEP results between the two species are due to similarities in the microanatomy or microphysiology of cortex. Conversely, they are not essentially determined by the topographic differences of visual projection areas. Thus, we think the alert macaque is an appropriate animal model that can help to understand the human VEP. With this in mind, we comment on the physiological basis of the observed similarities.

Spatial frequency tuning

Different groups of investigators have seen narrow and broad spatial frequency tuning. As they employed different methods, it is important to establish whether the different results are due to these differences. Our own results indicate that they are not. Using either method, either result can be obtained.

With one technique, plotting voltage vs spatial frequency for moderate to high contrast gratings, one obtains the most pronounced degree of narrow spatial frequency tuning (see Figs 2, 3, 5, and 7). This appears to be determined by the selective activation of the high contrast mechanism. For example, in Fig. 5A there is no evidence of a steep high contrast function at 0.55 and 4.5 c/deg, whereas it is very prominent at 6.7 and 10.3 c/deg. This selective activation leads to the very narrowly tuned high spatial frequency peak when high contrasts are used (in Fig. 2, electrode No. 2, and Fig. 5C). Conversely, there is no evidence of such sharp tuning when lower contrasts are used (bottom functions of Figs 5C and 7C), contrast levels where the low but not the high contrast mechanism is apparent.

When using the more tedious technique of extrapolating the lower limb of the contrast function to VEP threshold (Campbell and Maffei, 1970), the same applies. One can see broad tuning which approximates the psychophysics (Figs 5B and 8A). One can also see very narrow tuning by choosing a different electrode location or temporal frequency (Figs 7C and 8B).

Before discussing these results in neurophysiological terms, it is important to acknowledge and reject a type of interpretation that often crops up when considering the results of VEP research; specifically, the idea that the electrical cancellation of separate components yields spurious results. According to this interpretation, the narrow peaks are simply the algebraic sum of several broad components having nearly a 180° temporal phase shift. To deal with this potential criticism we have shown that double peaks can occur when the phases are essentially identical, not 180° apart (Tyler *et al.*, 1978). Furthermore, we also demonstrate that the narrow spatial frequency peaks can be isolated by stimulus manipulation (Nakayama *et al.*, 1982). Lastly, the existence of only one single peak in many of the monkey spatial frequency functions (see Fig. 2) does not admit to an electrical interaction hypothesis.

The existence of narrow spatial frequency tuning which has a spatial bandwidth more similar to individual cortical neurons (Movshon *et al.*, 1978; DeValois *et al.*, 1978) seems paradoxical. How can a mass potential, presumably recording from a large number of neurons, have characteristics more like a specific sample of neurons? Because these results seem so puzzling, we feel it necessary to offer two tentative hypotheses as an aid to guide future research:

(1) High frequency periodic stimulation is a relatively unnatural stimulus for the visual system. It is possible that a given class of cortical neurons with the same spatial frequency characteristics might also share a somewhat accidental set of temporal properties (delays, time constants, etc.). Thus, certain frequencies outside the normal range of stimulation might be unusually potent by causing "resonance-like" peaks. It should be noted, however, that by the term "resonance-like" we make no claim that the selectivity is similar to resonant peaks seen in second order linear systems. In fact, the lack of an additional phase shift through the peak of the temporal tuning function (see Fig. 3A) indicates that this linear explanation is inappropriate.

(2) The geometrical configuration of synaptic currents surrounding nerve cells in relation to the electrode is also important. Radially symmetric cells such as oculomotor neurons, for example, can undergo somatic depolarization but not be accompanied by an external voltage field (Baker and Precht, 1972). This is an experimental example of the "closed field" (Lorente de No, 1947). In other cells, the current field is asymmetric or dipolar, so that large potentials can be recorded at great distances.

If cellular elements with common spatial/temporal characteristics generated such open field dipoles, they could only be recorded at specific electrode locations, provided the dipoles had an oriented component relative to the electrodes. Our results make it conceivable that a combination of both these hypotheses can explain why SSVEP recordings accentuate the selectivity for particular temporal and spatial frequencies.

Origin of the two contrast functions

Our data indicate that the high contrast limb of the function relating log contrast and VEP amplitude deserves more attention. Campbell and Maffei (1970) suggested that it is a response to peripheral retinal stimulation, based on the failure to see it when macular small field stimuli and spatial frequencies above 3 c/deg were used. We find two reasons to reject this peripheral retinal stimulation hypothesis. First we found the high contrast function over a wide range of spatial frequencies (between 0.23 and 19 c/deg), thus covering high frequencies that are unlikely to be mediated by the peripheral retina. Furthermore, we also made a control experiment in monkey No. 1, restricting the stimulus field to a $2 \times 2°$ region surrounding the fovea. Despite the restricted field, the two limbs of the contrast function were still evident. Thus, our findings stress the existence of two limbs as a prominent and more general feature of the monkey VEP. Our description of these two limbs confirms observations made in humans using either transient (Kulikowski, 1977) or steady state VEP techniques (Apkarian and Tyler, 1982).

Consequently, we argue that this is a phenomenon in its own right, one which indicates that two distinct pattern mechanisms contribute to the generation of the surface VEP. As yet, there are no neurophysiological correlates of these two mechanisms at the level of the visual cortex. Their origin, however, could also be sub-cortical. Recent work on the monkey lateral geniculate nucleus shows that the contrast sensitivity thresholds of the cells in the magnocellular layers are much lower than those of cells in the parvocellular layers (Kaplan and Shapley, 1982; Blakemore, 1981). Therefore, the high contrast portion of the contrast function could be a striate or prestriate cortical reflection (either direct or indirect) of parvocellular LGN input, whereas the low contrast portion could be a cortical reflection of the magnocellular input to the cortex. This hypothesis clearly needs further experimental support, perhaps by obtaining contrast functions from direct VEP recordings in the parvo- and magnocellular layers of the LGN. It deserves attention insofar as it is one of the few identifiable surface VEP phenomena, which could be related to activity of highly specific sets of central visual neurons.

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