

CONTRAST ADAPTATION CAN INCREASE VISUALLY EVOKED POTENTIAL AMPLITUDE

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Summary—1. Prolonged inspection of a high-contrast sinewave grating increases the contrast required to detect gratings with similar spatial characteristics. It has been reported that a corresponding decrease occurs in the amplitude of visually evoked potentials (VEP) after such adaptation. These earlier investigations have been restricted to the use of low contrast test stimuli.

2. Contrary to these studies, we used a larger range of test contrasts to determine adaptation-dependent changes in the VEP-amplitude vs test contrast function. We measured VEP-amplitudes in response to phase-reversing test gratings of the same or different spatial frequency than that of the adapting grating. The results were compared to psychophysical thresholds determined for identical stimuli in the same observers measured during the same recording session.

3. In all 5 observers tested, we found an *increase* in the evoked potential amplitude following adaptation for test stimuli with a contrast above 0.07. This increase was specific to the spatial frequency and orientation of the adapting grating.

4. The dependence of the VEP-amplitude on the logarithm of test contrast was analysed before and after adaptation. The results indicate that the slope of the regression line describing this function significantly increased after adaptation. This suggests, that the contrast transducer function of the underlying neural mechanisms was changed by adaptation.

5. To explain the apparent discrepancy between psychophysical thresholds and evoked potential amplitudes after adaptation, we propose a model based on a shift toward higher contrast in the nonlinear contrast transducer function of the cortical neurones. Such a shift would lead to a reduction in the absolute response level but also to less response compression for high test contrasts and thus to greater VEP-modulation at the reversal frequency.

Key words—Spatial adaptation; contrast sensitivity; visually evoked potentials (VEP).

INTRODUCTION

Prolonged inspection of high-contrast sinewave gratings increases the contrast threshold for detecting gratings having a similar spatial frequency and orientation (Pantle and Sekuler, 1968; Blakemore and Campbell, 1969) and reduces the perceived contrast of subsequently presented gratings (Blakemore *et al.*, 1973; Georgeson, 1985). One of the first studies of spatial adaptation (Blakemore and Campbell, 1969) began by noting a decrease in the amplitude of the visually evoked potential following prolonged inspection of a high-contrast grating. These authors went on to explore the spatial frequency selectivity of this contrast threshold elevation using psychophysical techniques. Mecacci and Spinelli (1976) later studied the spatial frequency selectivity of changes in the VEP-amplitude following adaptation. Their findings suggested that, in parallel to psycho-

physical results, for low test contrasts the adaptation-dependent decrease in the VEP-amplitude was specific to the spatial frequency of the adapting grating. Similar findings for evoked potentials in the cat have more recently been reported by Bonds (1984).

It is well established that neurones in the visual cortex of cat and monkey exhibit adaptation effects following prolonged stimulation by high contrast stimuli (Maffei *et al.*, 1973; Movshon and Lennie, 1979; Dean, 1983; Albrecht *et al.*, 1984; Sclar *et al.*, 1985). Ohzawa *et al.* (1985) specifically studied the effects of contrast adaptation from the perspective that adaptation is a form of *contrast gain adjustment*. They found neurones which exhibited a shift of the contrast transducer function towards higher contrast levels. Greenlee and Heitger (1988) explored adaptation-dependent changes in psychophysically determined incremental contrast thresholds for different pedestal contrast

levels. Contrary to the original claim by Barlow *et al.* (1976), Greenlee and Heitger (1988) found that incremental contrast thresholds decreased following adaptation. Their finding suggested that a similar form of contrast gain adjustment occurs in the human visual cortex. The present investigation was conducted to explore whether an electrophysiological correlate of such a process could be found in the human visual evoked potential.

METHODS

Grating stimuli were created on a cathode ray tube (Tektronics 602) having a white (P4) phosphor and a refresh rate of 200 Hz. The spatial frequency, phase, orientation and contrast of the gratings were defined by an image generator (Innisfree Inc.) under computer control. The contrast of the sinewave grating was defined by the equation:

$$C = (L_{\max} - L_{\min}) / (L_{\max} + L_{\min});$$

where L_{\max} and L_{\min} represent the maximal and minimal luminance levels in the grating. The space-averaged luminance of the grating was 20 cd/m^2 and it subtended $12 \times 10 \text{ deg}$ of visual angle at the eye, with a viewing distance of 57 cm. Viewing was binocular with natural pupils. The observer rested his or her chin and forehead on a support to assure constant viewing distance and head orientation. The spatial phase of the grating was shifted by 180 deg phase angle 7.8 times per second (corresponding to a temporal frequency of 3.9 Hz) as a squarewave function of time.

Visually evoked potentials were recorded using silver-cup scalp electrodes which were positioned 2.5 cm rostral of the inion and referenced to the right ear. The observer's left ear was grounded. Electroencephalographic activity was amplified (Toennies Inc.) using bandpass filtering with 1.6 and 30 Hz corner frequencies, and a slope of 6 dB/octave. Digital conversion of the analog signals was performed with 10-bit resolution and a sampling rate of 500 Hz. Sweeps of 512 ms duration were averaged and displayed on-line using a microprocessor (see Fig. 1a). Averaged records were based on a total of 80 sweeps per subject and condition. To reduce the effect of decay of adaptation (in the adapted state) or of adaptation to the test grating (in the unadapted state) these records were divided into four blocks of 20 sweeps each with interleaved readaptation or rest pauses,

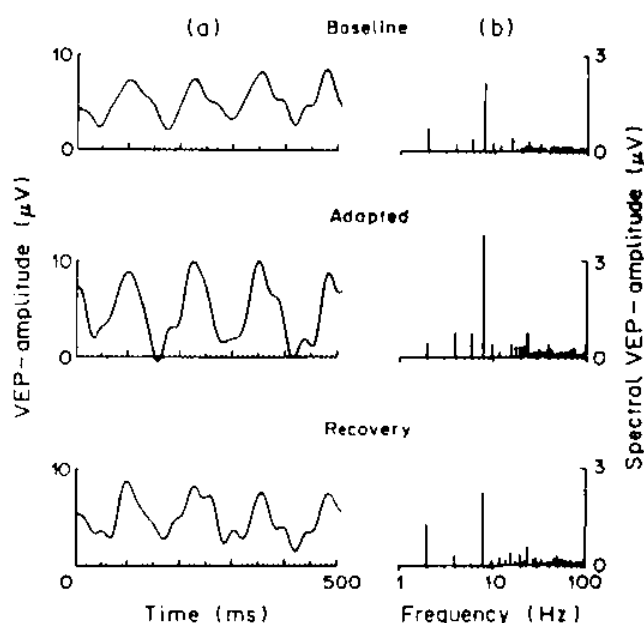


Fig. 1. (a) Electrophysiological recordings of visually evoked potentials shown as a function of time for the average of four blocks consisting of 20 sweeps each and (b) their Fourier spectrum. During each sweep, the test grating reversed its spatial phase 3.9 times corresponding to a reversal frequency of 7.8/s. The spatial frequency of the sinewave test grating was 2 c/deg, the orientation was vertical and the contrast was 0.16. The upper trace was recorded in this subject (B.B.) after 20 min light adaptation to a blank screen. The middle trace was recorded after 20 min adaptation to a grating pattern having a spatial frequency of 2 c/deg, a reversal frequency 7.8/s and a contrast of 0.4. The final trace shows the responses to the test grating after 20 min recovery from pattern adaptation.

respectively. An adjustable artifact threshold (usually $30 \mu\text{V}$) was set so that any sweeps containing amplitudes exceeding this value (due to blinking, etc.) were automatically rejected. All other sweeps were included in the data analysis. To facilitate Fourier transformation (FT) of the averaged steady-state potentials and to reduce spillover, the phase-reversal rate was adjusted so that exactly 4 events occurred in each sweep. Averaged records consisting of 80 sweeps were subjected to FT. The amplitude of the evoked potential was estimated based on the magnitude of the Fourier component at the phase reversal frequency. To enhance comparison across observers, signal amplitude was normalized by fitting a regression line to each subject's baseline data and dividing all raw data points by the predicted amplitude for the highest contrast used (0.23).

Before and after adaptation and after recovery from adaptation, psychophysical thresholds were determined during the same recording session using the method of adjustment. The contrast of the test grating was increased until the observer could just detect the presence of the

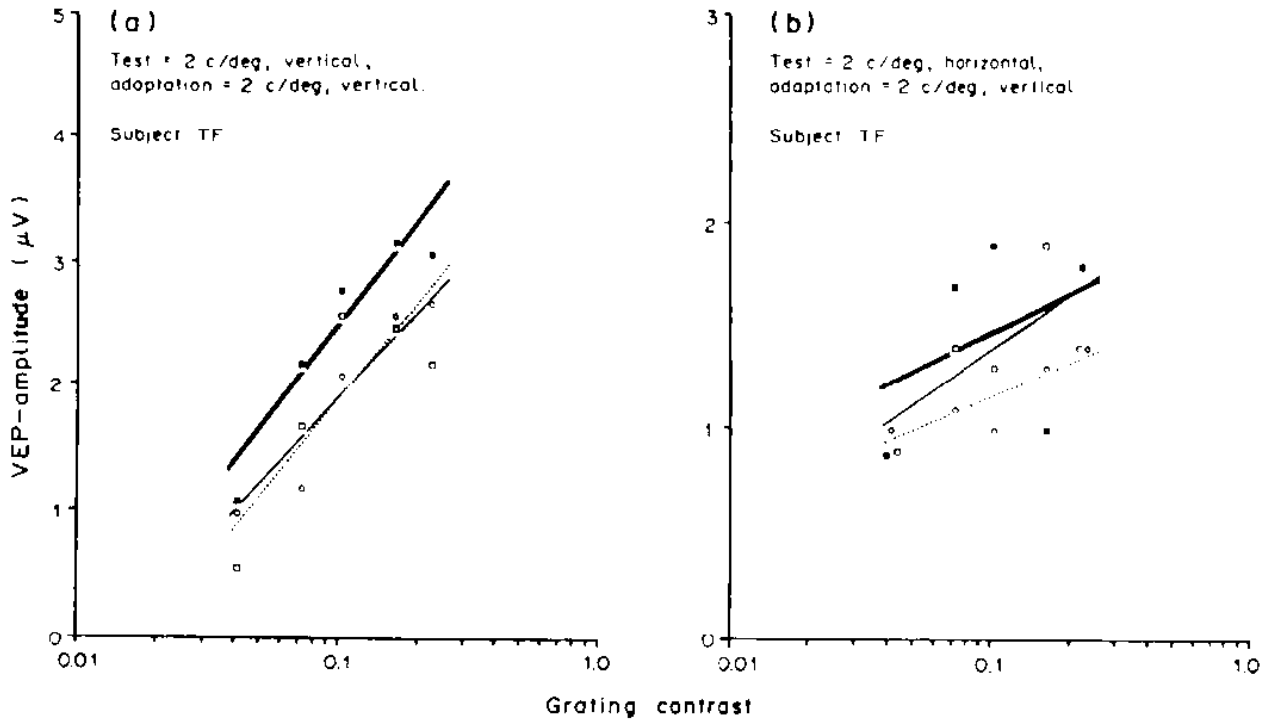


Fig. 5. VEP-amplitude (in μV) shown as a function of the test contrast before and after adaptation to a vertically oriented grating of 0.4 contrast and 2 c/deg spatial frequency. (a) Shows the results for the condition where the adapting and test grating shared the same orientation and spatial frequency and (b) gives the results for the condition where the orientation of the test grating was orthogonal to that of the adapting grating. Results from subject T.F.

DISCUSSION

The present findings indicate that adaptation to luminance modulated sinewave gratings elicits an *increase* in the amplitude of the visually evoked potential recorded on the observer's scalp for test contrasts above 0.07. The elevations in VEP-amplitude are specific to

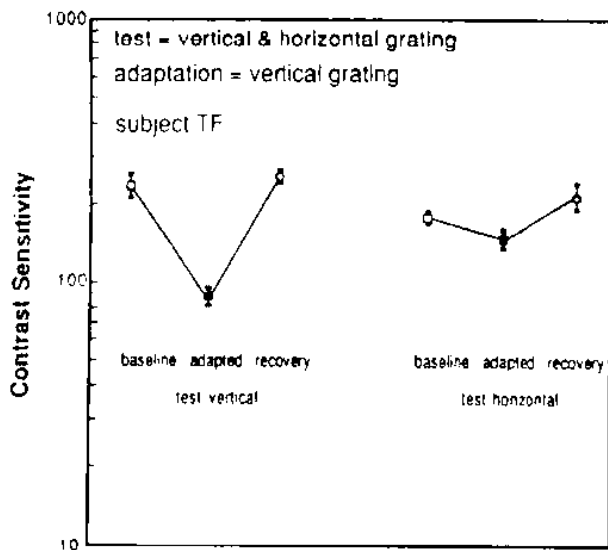


Fig. 6. Contrast sensitivity before (\square) and after (\blacksquare) adaptation to a vertically oriented grating of 2 c/deg, and after recovery from this adaptation (\diamond) for a vertical test grating (left) and a horizontal test grating (right) in the same subject as in Fig. 5.

the spatial frequency and the orientation of the adapting grating as found for the reduction in contrast sensitivity measured in the same observers in the same recording session. Earlier investigations found a *decrease* of VEP-amplitude after adaptation (Blakemore and Campbell, 1969; Mecacci and Spinelli, 1976).

As our intention was not to perform an identical replication of the earlier investigations, some of our stimulus parameters and some details of the recording technique differ from those used by the earlier investigators. Although the active electrode was placed in our experiments in the same position as that used in the Blakemore and Campbell (1969) and the Mecacci and Spinelli (1976) studies, our reference electrode was placed on the right ear, whereas Blakemore and Campbell and Mecacci and Spinelli placed theirs 2.5 cm temporal of the active electrode. In an attempt to copy this recording technique, and thus to control for the possibility that the different findings were due to the varying electrode placements, we tested one subject using two different reference electrodes at the same time, one on the right ear and one 2.5 cm from the active electrode. In this way, we could compare the VEP-amplitude in the same observer for the two different electrode placements. The results of this control

experiment revealed that the Blakemore and Campbell placement yielded overall smaller amplitudes, which, however, were less noisy. After adaptation we still found an increase in the VEP-amplitude with a test contrast of 0.1.

An important difference in this study compared to the earlier investigations is that we varied the contrast of the test gratings from 0.02 to 0.23. Blakemore and Campbell (1969) used a single test contrast which was 0.7 log units above the observer's contrast threshold. Assuming that this threshold was around 0.007 (corresponding to a contrast sensitivity of 140), the test contrast in the Blakemore and Campbell (1969) study was probably around 0.035. As can be seen in Fig. 4, for test contrasts below 0.07, we found a slight *decrease* in the evoked potential amplitude. Mecacci and Spinelli (1976) used a slightly higher test contrast of 0.08 and an adapting frequency that was one octave above that used in this study (4 vs 2 c/deg). Adapting time and adapting contrast was the same in both studies. For a test contrast of 0.07 and a test frequency of 2 c/deg we found that more than half of the recorded samples increased in amplitude, while the other half either remained unchanged or were slightly decreased following adaptation; these differences were not observer-specific but rather due to sampling noise (see Fig. 4). We thus believe that the Mecacci and Spinelli (1976) findings can be best explained by the fact that these authors used a low test contrast in conjunction with a higher adapting frequency.

The increase found here in the VEP-amplitude following adaptation appears puzzling when one considers recent work using the adaptation paradigm with single unit recording in the visual cortex of the cat (Dean, 1983; Albrecht *et al.*, 1984; Ohzawa *et al.*, 1985) and the kitten (Sclar *et al.*, 1985). All of these findings indicate that the spike frequency generally declines following adaptation. Ohzawa *et al.* (1985) suggested that this decline might reflect a *contrast gain adjustment* in the neurones responding to the contrast in the adapting grating. These authors used a paradigm first employed by Bodis-Wollner *et al.* (1972), where the contrast of a sinewave grating was modulated over time and the just-noticeable difference in the contrast modulation (or delta spike frequency in single units) was measured for varying background contrast levels. The introduction of a brief adaptation period appears, according to Ohzawa *et al.*'s (1985)

findings, to *improve* the ability of the underlying mechanisms to encode contrast differences at high contrast levels. According to their findings, the contrast transducer function, having a non-linear compressive *s*-shape, shifts towards higher contrast levels after adaptation. Using a psychophysical contrast discrimination paradigm, Bodis-Wollner and Hendley (1979) found that adaptation to a high contrast grating shifts the modulation sensitivity functions toward higher contrast levels. More recently, Greenlee and Heitger (1988) found that spatial adaptation enhances incremental contrast discrimination for contrast levels greater than 0.4. Contrast adaptation, therefore, appears to shift the semi-saturation constant of mechanisms sensitive to low contrast levels towards higher contrast levels. This implies that test contrasts high enough to reach the saturating part of the contrast transfer function before adaptation will operate within a more linear segment of this function after prolonged adaptation. This result applies to both single-cell (although mostly based on cat) as well as psychophysical findings and corresponds to lower neuronal activity in the adapted state. Does this imply that adaptation should reduce VEP-amplitude? In order to interpret VEP findings one first requires a model to link neuronal events to surface potentials (Creutzfeldt and Kuhnt, 1973). Unfortunately, there are a number of problems involved in such a venture: first, the steady-state VEP does not allow discrimination between action potentials, IPSPs or EPSPs. Second, steady-state responses correspond not to single-unit activity *per se*, but rather to stimulus-synchronized *modulation* of neuronal mass activity. With these drawbacks in mind, we present a tentative model, shown schematically in Fig. 7, to account for our apparently conflicting findings.

The temporal square-wave contrast reversal of the input stimulus is lowpass filtered at an early stage in the visual system (retina) and assumed to take a sinusoidal shape (Fig. 7, top panel). This is passed to a full-wave rectifier which may be situated in the retina, as the pattern-ERG, like the VEP, is dominated by the second harmonic of the stimulus frequency. The exact locus of rectification is, however, unimportant for this model. The neural response (middle panel) results from the action of the contrast transducer function. Depending on stimulus contrast and adaptive state, the activity is more or less strongly compressed by the saturating contrast transducer function of the active

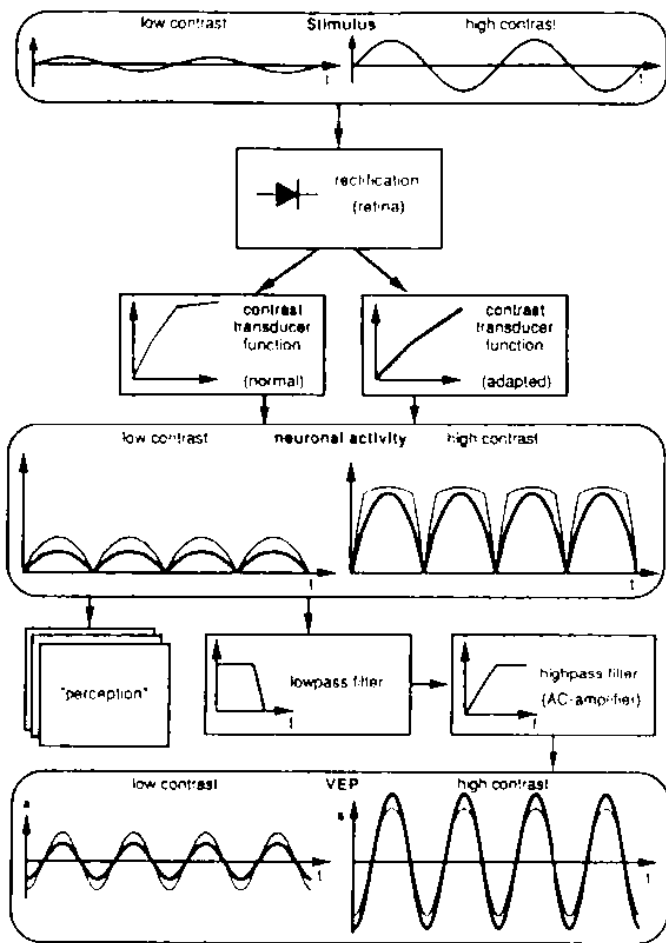


Fig. 7. A hypothetical model put forth to explain the apparent discrepancy between the adaptation-dependent change in VEP-amplitude and the change in contrast sensitivity. The rectangular panels represent processing and filtering stages, the panels with rounded corners represent simulated activity for low contrast (left) and high contrast gratings (right). Thin lines correspond to the unadapted state, thick lines to the adapted state. For more details see text.

cortical mechanisms. In the adapted state (thick lines), the *average* mass neural activation is lower than in the unadapted state (middle panel: thick vs thin curve). However, the spectral composition of this average activity over time differs between normal and adapted states, such that in the adapted state more energy is concentrated at the reversal frequency compared to higher frequencies. Therefore, after lowpass filtering, the resulting a.c.-amplitude in the adapted state (right bottom panel, thick trace) is higher than in the unadapted state (thin trace). The mean value of the neural activity (i.e. the d.c.-level) is lower in the adapted state, but the mean value does not show up in a steady-state VEP, only its modulation. For low test contrast levels (left), there is less compressive action; consequently, after filtering, the

amplitude in the adapted state remains lower than in the unadapted state.

The model was implemented on a computer and has several free parameters. The unadapted and the adapted state, however, differ only in one parameter: the shift of the contrast transducer functions of the adapted neural mechanisms was simulated by a 50% gain attenuation of the input signal. Such an attenuation reduces the response compression for high contrast stimuli. Simulation results for two arbitrary contrast levels differing by a factor of 4 are depicted in Fig. 7.

The model explains the decrease of VEP-amplitude caused by adaptation for low test contrasts and for the increase in amplitude elicited by adaptation for high test contrasts. It predicts that the harmonic distortion (due to the compressive part of the contrast transducer function) should be lower in the adapted state. We performed a reanalysis of our data concerning this point, the results of which are shown in Fig. 8 for the highest contrast used (0.23). The distortion index was defined as the response magnitude at 15.6 Hz (twice the reversal frequency) divided by the amplitude at 7.8 Hz (the reversal rate) for each condition separately. The results indicate that the relative second harmonic distortion is significantly reduced following adaptation ($p = 0.05$, one-tailed). For a test contrast of 0.16 the effect is similar but less pronounced.

The model thus accounts for both the psychophysical and VEP-data measured under the adaptation and testing conditions used here. It implies that VEP-data need not necessarily correspond to suprathreshold contrast perception, although a lawful relationship may

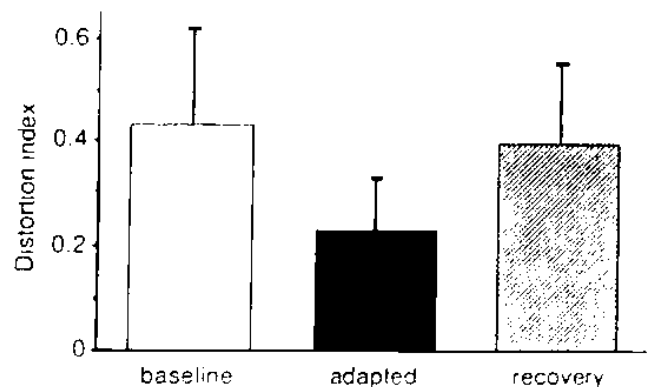


Fig. 8. The relative second harmonic distortion (amplitude at 15.6 Hz/amplitude at 7.8 Hz) calculated for each subject and each condition separately. Mean distortion index values averaged over 5 subjects + 1 SEM are shown for the highest test contrast used (0.23).

exist between these two domains (Regan and Spekreijse, 1986).

In conclusion, the present results indicate that prolonged adaptation to suprathreshold gratings increases the amplitude of the visually evoked potential for medium to high test contrasts. The spatial frequency and orientational selectivity of this increase correspond approximately to the decreased sensitivity found with psychophysical methods and may reflect a shift in the semi-saturation constant of the contrast-transducer function of the underlying neural mechanisms, with consequently less response compression. The findings suggest that earlier models linking VEP-amplitude to psychophysical findings before and after adaptation may only hold for near-threshold contrast levels. Such adaptation-dependent changes in VEP-amplitude should be kept in mind by the clinical electrophysiologist, who relies on relative amplitude differences to gain insight into physiological and pathological processes in the human visual system.

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