

Human cortical responses to contrast modulations of visual noise

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Received 20 September 2004; received in revised form 8 February 2005

Abstract

We studied visual evoked potentials (VEPs) elicited by second-order contrast modulations of binary dynamic noise and first-order luminance modulations. Using a 3-point Laplacian operator centred on Oz, we found that contrast modulations of both low and higher spatial frequencies elicited a negative component whose latency was about 200 ms. The latency of this component was significantly longer than that of the early Laplacian components to first-order luminance modulations. These findings could be due to slower first-stage linear filters and additional processing stages of the second-order pathway. The topographical analysis of scalp recorded VEPs to central and half-field stimulation has suggested that the responses to second-order patterns are likely to be generated by neuronal structures within the primary visual cortex which may have inputs from extrastriate neurons via feedback connections.

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Keywords: Visual evoked potentials; Second-order vision; Visual cortex

1. Introduction

Much of our understanding of visual perception is based on studies of visual responses to patterns which are defined by spatiotemporal variations in luminance (first-order cues). The processing of luminance modulations is conventionally attributed to linear filtering by cells in the early visual cortex that respond selectively to patches of various spatial frequencies and orientations (e.g. see De Valois & De Valois, 1990). Visual patterns can also be defined by modulations of second-order image cues, such as carrier contrast or local orientation. However, second-order large-scale modulations of a carrier (e.g. visual noise composed of fine random elements) do not contain differences in average lumi-

nance and so cannot be captured by linear luminance filters. The study of second-order vision can therefore provide additional information on visual information processing.

Contrast modulations can be extracted by linear filters if they follow a non-linearity which gives rise to first-order distortion products at the modulation frequency of the second-order stimuli. Psychophysical and electrophysiological studies of second-order motion and pattern processing (Cavanagh & Mather, 1989; Chubb & Sperling, 1998; Schofield & Georgeson, 1999; Wilson, Ferrera, & Yo, 1992; Zhou & Baker, 1993) have suggested that second-order modulations are processed by a non-linear pathway which consists of first-stage linear filters, followed by a non-linearity and second-stage linear filters (“filter-rectify-filter” model). The “filter-rectify-filter” model assumes that additional stages are involved in the processing of second-order information compared to first-order information. This suggests that responses to contrast modulations require a longer

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processing time than those to luminance modulations (Wilson et al., 1992; Yo & Wilson, 1992). Indeed, studies have shown that envelope-responsive simple neurons in area 18 respond more slowly to second-order modulations (Mareschal & Baker, 1998).

This concept raises the question of the neuronal representation of the mechanisms processing second-order information. Zhou and Baker (1993) found that neurons in cortical areas 17 and 18 of the cat responded to stimulus attributes that have no corresponding luminance modulations. Their stimuli consisted of a carrier (a stationary high spatial frequency grating) whose contrast was modulated by an envelope (a moving low spatial frequency grating). The results showed that about 30% of the tested cells responded significantly to the envelope. The neurons in the extrastriate area 18 of cat are more likely to be envelope responsive than neurons in the striate cortex. On the other hand, the same neuron exhibited different optimal spatial frequencies for luminance gratings and envelopes. This result has ruled out the simple explanation that an early non-linearity (e.g. in the photoreceptors) precedes spatial frequency-selective filtering. Further, psychophysical results do not support this hypothesis (Cropper, 1998; Derrington & Badcock, 1986; Henning, Hertz, & Broadbent, 1975; Nachmias & Rogowitz, 1983; Scott-Samuel & Georgeson, 1999). Therefore, the filter-rectify-filter stream is likely to have a cortical origin.

In macaques, 9% of V1 neurons and 25% of MT neurons respond to both first- and second-order motion patterns (O'Keefe & Movshon, 1998). The notion that the first- and second-order information is processed separately by extrastriate cortical areas has been supported by human lesion studies. Studies reported that two patients showed evidence of a double dissociation of impairments of first-order and second-order motion processing (Vaina & Cowey, 1996; Vaina, Cowey, & Kennedy, 1999; Vaina, Makris, Kennedy, & Cowey, 1998). Greenlee and Smith (1997) measured sensitivity to orientation, direction and speed of motion of first- and second-order patterns in patients with various cortical lesions. They concluded that the mechanisms which detect the speed of first- and second-order modulations share common extrastriate locations. However, there was evidence to suggest that the two pathways are, at least in part, separate. In addition to the extrastriate involvement, recent fMRI studies suggest that second-order motion stimuli may be processed as early as V1 (Nishida, Sasaki, Murakami, Watanabe, & Tootell, 2003; Seiffert, Somers, Dale, & Tootell, 2003).

The non-invasive method of visual evoked potentials has been used to study human cortical responses to second-order stimuli. Previous studies have reported a specific texture-segregation component of VEPs to patterns defined by gradients along orientation of line ele-

ments (Bach & Meigen, 1992, 1998–1999; Lamme, Van Dijk, & Spekreijse, 1992), spatial frequency (Bach, Schmitt, Quenzer, Meigen, & Fahle, 2000) and motion (Lamme, Van Dijk, & Spekreijse, 1994). In these studies, the VEPs elicited by the onset of second-order patterns have been regarded as a linear sum of a component which is specific to the texture segregation and a “low-level” response to first-order local features. The texture specific component is isolated by calculating the difference between the VEP to the onset of a pattern defined by texture and the VEP to the onset of a uniform expression of the particular visual dimension. The results have shown that thus derived texture VEPs contain a negative component whose latency is about 200 ms.

In theory, modulations of carrier contrast do not contain first-order Fourier components at the modulation frequency of the second-order pattern. Therefore, VEPs elicited by contrast modulations of a carrier provide a useful means to record isolated responses to second-order stimuli. Elleberg et al. (2003) recorded VEPs to the onset of drifting luminance and contrast modulations of static binary noise. The VEPs to first-order motion contained an early positive component and a following negative component which usually are associated with the activity of pattern and motion processing mechanisms, respectively (Bach & Ullrich, 1994; Kubova, Kuba, Spekreijse, & Blakemore, 1995). The results showed that the VEPs to second-order motion had a waveform similar to those elicited by first-order motion, however, both the early and later components were slower than the corresponding components of the VEPs to luminance modulations. The authors suggested that their findings could be accounted for by the presence of additional processing stages in both second-order pattern and motion processing mechanisms as compared to the corresponding first-order mechanisms.

The aim of the present study was to investigate VEPs elicited by the onset of stationary contrast modulations of dynamic noise. In contrast to motion VEPs (Bach & Ullrich, 1994; Elleberg et al., 2003; Kubova et al., 1995), which reflect activity of both pattern and motion processing mechanisms, we chose simpler, stationary patterns as VEPs to stationary stimuli are generated mainly by pattern processing mechanisms. We were interested in VEPs to contrast modulations of low and higher spatial frequencies, and the distribution of these responses on the scalp. Further, we investigated the possibility of V1 involvement in the processing of these second-order stimuli.

Experiment 1 was aimed at determining the prominent and repeatable components of the responses to contrast modulations of low and higher spatial frequencies. We used multiple-channel recording in order to investigate the spatial distribution across the scalp of VEPs and Laplacian responses (Manahilov, Riemsdag,

& Spekreijse, 1992; Srebro, 1985) elicited by contrast modulations. We compared the responses to second-order contrast modulations with those evoked by first-order patterns (luminance gratings and luminance gratings embedded in dynamic noise). The use of two types of first-order stimuli was aimed at separating effects due to the type of modulations from those due to the presence of noise. In particular, we hypothesised that the responses to contrast modulations would have a longer latency than those to luminance modulations (Mareschal & Baker, 1998; Wilson et al., 1992; Yo & Wilson, 1992).

Single cell (O'Keefe & Movshon, 1998; Zhou & Baker, 1993) and fMRI (Nishida et al., 2003; Seiffert et al., 2003) studies have demonstrated that V1 neuronal structures are involved in the processing of second-order information. Using our knowledge of the architecture of the visual system, we tested whether the sources of the responses to contrast modulations are generated by the primary visual cortex. According to the cruciform model of the primary visual cortex (Jeffreys & Axford, 1972; Spekreijse, Estevez, & Reits, 1977), the projections of upper and lower visual fields face one another across the calcarine fissure, while the projections of the left and right visual fields face each other across the midline fissure. Therefore, stimulation of the upper/lower or left/right areas of the visual field would generate activities which could be approximated by electrical dipoles of geometrically opposite orientations and so produce electrical responses of opposite polarity. Previous studies have shown that quadrant field stimulation results in polarity reversal of the early component of VEPs elicited by gratings of middle and higher spatial frequencies (Parker, Salzen, & Lishman, 1982a) which suggests that the generators of this component are located in the striate cortex. In Experiment 2, we carried out multiple-channel recording of VEPs to contrast modulations which were presented in the upper, lower, left or right parts of the visual field in order to determine whether the sources of the prominent VEP component have a striate origin.

Finally, in a control experiment we used static noise as a carrier in order to test whether VEPs to supra-threshold contrast modulations of static noise contain components evoked by first-order luminance changes which accompany the modulation of carrier contrast.

2. Methods

2.1. Subjects

We tested seven subjects (five female, two male) having normal or corrected-to-normal vision. Informed consent was obtained from each subject before enrolment in the study.

2.2. Apparatus and stimuli

Stimuli were generated by a PC on a 19 in. RGB monitor (Vision Master Pro 450, Iiyama Electronics America, Inc.) at a resolution of 640×480 pixels and frame rate of 120 Hz. A custom video summation device (Pelli & Zhang, 1991) was used to produce 256 grey levels with a 12-bit precision.

Three stimulus types were used (diagrams illustrating the stimuli and their one-dimensional profiles are shown in Fig. 1):

- (i) Luminance grating: $I(x, y) = I_0[1 + l \sin(2\pi x f_x)]$, where f_x is the spatial frequency, l is the contrast, and I_0 is the mean luminance.
- (ii) Luminance modulations: vertical luminance grating added to 2D binary noise: $I(x, y) = I_0[1 + nN(x, y) + l \sin(2\pi x f_x)]$, where n is the contrast of the noise $N(x, y)$.
- (iii) Contrast modulations: 2D binary noise carrier $N(x, y)$ whose contrast (n) was modulated by a vertical grating: $I(x, y) = I_0[1 + nN(x, y) + nN(x, y) m \sin(2\pi x f_x)]$, where m is the modulation depth of the second-order signal and the term $nN(x, y) m \sin(2\pi x f_x)$ represents the multiple side-band components due to the multiplication of a noise sample by a modulating sinusoidal signal (Schofield & Georgeson, 1999).

When dynamic noise was used, the noise samples were selected randomly from a set of 20 noise samples. They were updated every other monitor frame (frequency of 60 Hz) and matched only within pairs of monitor frames. In the case of static noise, a single randomly selected noise sample was used in a block of trials.

The stimuli were motionless and were presented in on/off mode at 0.7 Hz (signal and blank intervals of 700 ms each). Typically, the duration of a block of trials was 45 s. When VEPs to luminance and contrast modulations were recorded, the blank intervals contained non-modulated noise samples. In the case of luminance gratings, the signal was presented on a grey background. The phase of the modulating signal was randomized across trials. The stimuli had a circular form (diameter of 8 deg). The stimulus contrast in the central part of the stimulation field was multiplied by 1.0 across a circular region of 8-deg diameter and then it was damped smoothly by a cosine function (half-period of 1 deg). The screen pixel size was $1'$. The r.m.s. contrast of the binary noise was 0.4. The mean luminance of the monitor was 30 cd/m^2 . The viewing distance was 171 cm.

The monitor's gamma non-linearity was calibrated by an OptiCal photometer (Cambridge Research System Ltd.) interfaced to the PC and the calibration was verified every few weeks. We found that the mean luminance of horizontal and vertical square-wave gratings whose

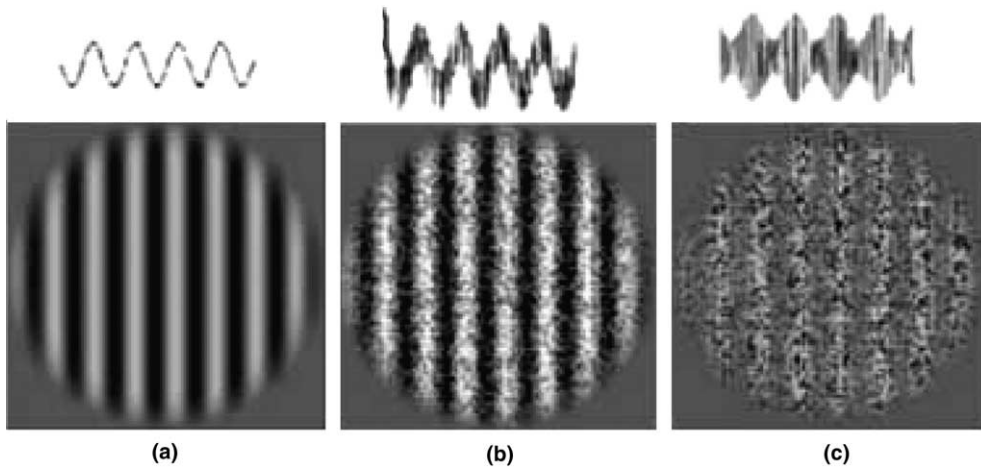


Fig. 1. Illustration of stimuli together with the one-dimensional profile for (a) luminance grating (a) luminance grating embedded in noise (b) and contrast modulated noise (c).

half period consisted of two screen pixels did not vary as a function of grating contrast up to 0.95, implying insignificant adjacent pixel non-linearity (Klein, Hu, & Carney, 1996). Therefore, we used noise pixels which consisted of four screen pixels ($2 \times 2'$).

2.3. VEP recording and analysis

VEPs were recorded and analysed by custom software using multi-channel amplifiers (Contact Precision Instruments) and a 64-channel data acquisition board PCI-DAS6402/16 (Computerboard Ltd.). The EEG signals were recorded by Ag/AgCl sintered ring electrodes mounted on an electrode cap (EasyCap, FMS), amplified within the 0.3–100 Hz band and digitised at a rate of 1000 Hz. Electrode impedance was below 10 kΩ. In order to measure the pattern onset VEP, the recording epoch was 450 ms which started 50 ms prior to the stimulus onset.

VEPs were measured at PO7, Oz and PO8 (Fig. 2) with reference to the right earlobe. The ground electrode was on the left earlobe. 3-point Laplacian transforms (L) were calculated using the following equation (Hjorth, 1975; Manahilov et al., 1992; Srebro, 1985):

$$L = (2A_{Oz} - A_{PO7} - A_{PO8})/d^2, \tag{1}$$

where A_{Oz} , A_{PO7} and A_{PO8} denote the response amplitudes measured at Oz, PO7 and PO8 and d is the distance between the centre electrode and the outer electrodes. Thus determined the Laplacian response represents the linear second spatial derivative of the potential field which is a measure of the component of electrical current flowing normal to the surface of the scalp (units $\mu\text{V}/\text{cm}^2$). The amplitudes of the Laplacian components were measured from the baseline defined as the mean value of the traces before the stimulus onset (50 ms) to the corresponding peak or trough. At least 60

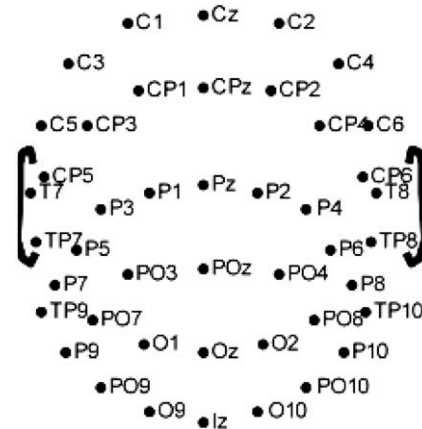


Fig. 2. Layout of 44 electrodes located over occipital, temporal, parietal and central cortical areas which were used to record VEP maps. Figure faces upwards.

sweeps to each stimulus were averaged and four recordings on different days were taken from each subject.

We also recorded EEG signals from 44 electrodes over occipital, temporal, parietal and central cortex with reference to the left earlobe (Fig. 2). VEPs were digitally re-referenced to the averaged earlobes. These data were used to generate a denser voltage map by means of a cubic spline interpolation. The scalp voltage maps were used to construct surface Laplacian (scalp current density) maps by using a 2D finite difference approximation of Laplace’s differential operator (Matlab, Mathworks Inc).

2.4. Psychophysical procedure

Detection thresholds for luminance and contrast modulations were measured using a staircase method and a 2IFC procedure (Manahilov, Calvert, & Simpson,

2003). Each trial consisted of two 2000-ms intervals which were marked by a tone and separated by a 500-ms gap (mean luminance). One of the intervals, randomly selected, contained a signal; the other interval had no signal. Noise images were displayed throughout each 2000-ms interval with abrupt onsets and offsets. The signal was displayed in a 700-ms rectangular temporal window which started 700 ms after the onset of the 2000-ms signal interval. The subject's task was to fixate the centre of the stimuli and identify the interval that contained the signal by pressing one of two buttons. Each staircase started at a suprathreshold contrast level of the signal with a contrast step of 0.2 log units. After each staircase reversal, the step size was halved and this process continued until the step size became 0.05 log units. The subsequent eight staircase reversals were collected and the threshold measure was the mean of these estimates. The mean values of the threshold contrasts for every experimental condition were calculated by averaging data collected in three experimental sessions.

3. Results

3.1. Contrast threshold measurements

In order to equate the visibility of the luminance and contrast modulated stimuli presented during the VEP experiments, we measured threshold contrasts for detection of luminance and contrast modulations as ex-

plained in the Methods section. We found that the mean threshold contrasts ($\pm 95\%$ CI) across the subjects were: 0.025 (± 0.008) and 0.032 (± 0.008) for 0.5- and 4-cpd luminance gratings embedded in dynamic noise, respectively; and 0.22 (± 0.08) and 0.225 (0.10) for contrast modulations of dynamic noise of 0.5- and 4-cpd, respectively. When static noise was used as a carrier, the mean threshold contrast was: 0.20 (± 0.06) and 0.21 (± 0.08) for 0.5- and 4-cpd contrast modulations, respectively.

3.2. Experiment 1

In this experiment we sought to determine the prominent components of VEPs to contrast modulations of 2D dynamic noise and compare them to those of VEPs elicited by luminance modulations.

3.2.1. Topographical maps of responses to first- and second-order patterns

We measured the spatial distribution across the scalp of the most prominent early and later components of VEPs and Laplacian derivations evoked by luminance gratings and contrast modulations. Figs. 3 and 4 illustrate results from one subject (JC) which were similar to the data of another subject (KF).

3.2.1.1. Early components. The first pronounced component of the VEPs recorded at Oz to contrast modulations of both 0.5 and 4 cpd had a negative polarity

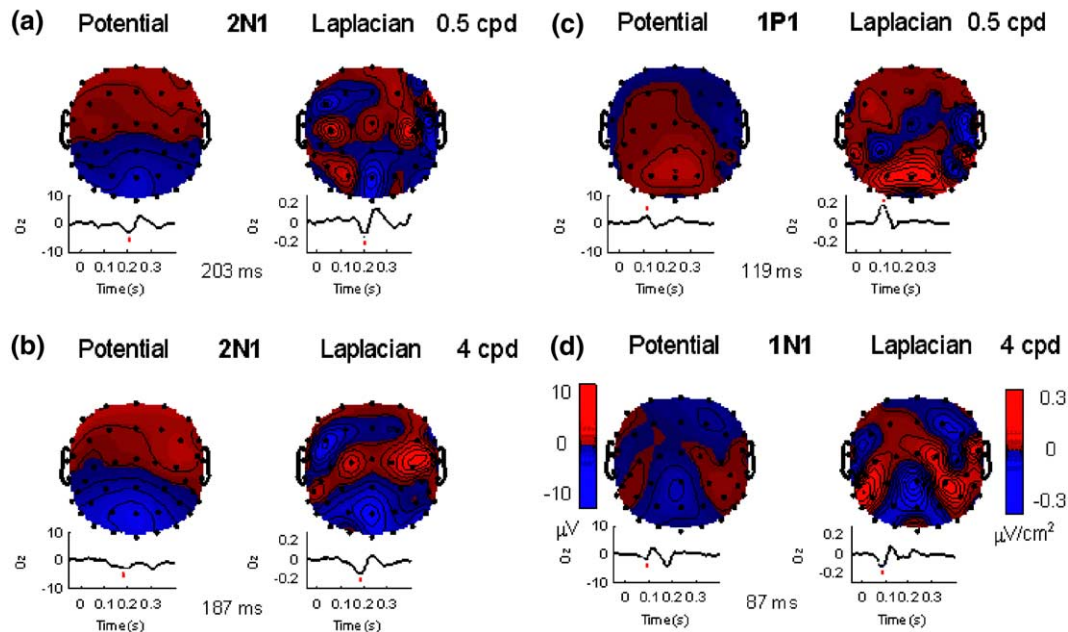


Fig. 3. Potential and Laplacian maps of the early component 2N1 (the prefix “2” represents second-order modulations) of the responses to contrast modulations of dynamic noise (contrast 0.9) of 0.5 cpd (a) and 4 cpd (b) and the early components 1P1 (the prefix “1” represents first-order stimuli) and 1N1 of the responses to gratings (contrast 0.1) of 0.5 cpd (c) and 4 cpd (d), respectively. The traces under the potential maps illustrate the VEPs recorded at Oz; the traces under the Laplacian maps show the Laplacian responses calculated by means of a 3-point Laplacian operator [Eq. (1)]. The markers on the traces denote the latencies of the early components. Data of subject JC.

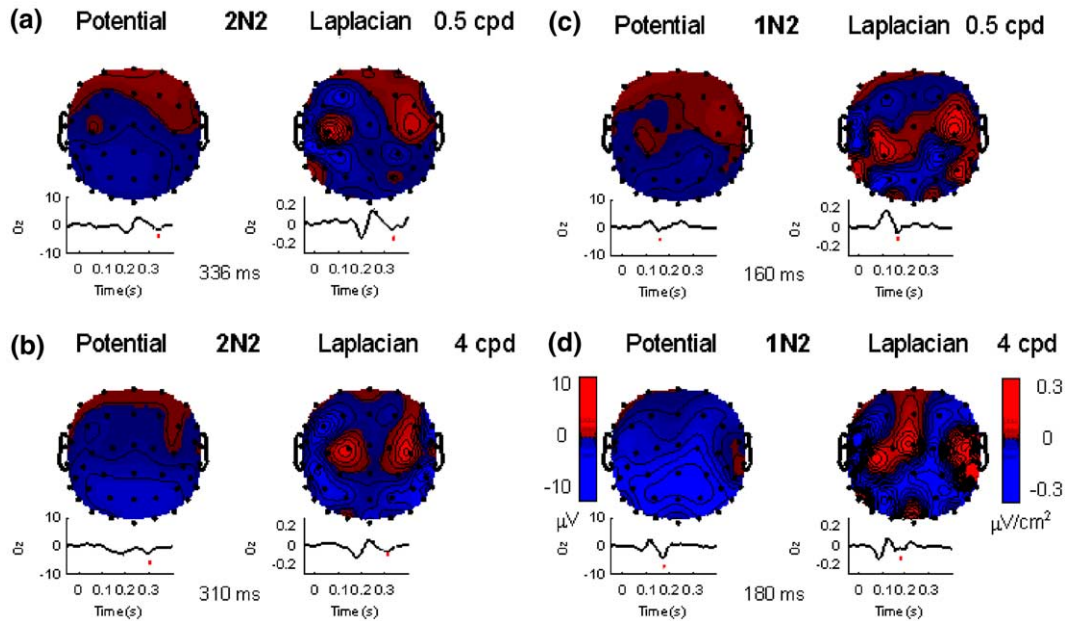


Fig. 4. Potential and Laplacian maps of the later component 2N2 of the responses to contrast modulations of 0.5 cpd (a) and 4 cpd (b) and the later component 1N2 of the responses to gratings of 0.5 cpd (c) and 4 cpd (d). The other designations are as in Fig. 3. Data of subject JC.

and a latency of around 200 ms (Fig. 3a and b, left traces). We denote this component by 2N1 where the prefix “2” stands for the stimulus type (second-order modulations). The VEP maps (Fig. 3a and b, left maps) recorded at latencies of 203 ms and 187 ms for contrast modulations of 0.5 and 4 cpd, respectively, show that the negative potential field occupies a large area peaking around the occipital site Oz. The Laplacian maps (Fig. 3a and b, right maps) exhibit a more restricted distribution of negativity which is surrounded by positivity.

These results are consistent with previous model calculations using a radially oriented dipole in the cortex which have shown that the potential amplitude on the scalp has a broader spatial distribution as compared to the spatial distribution of the Laplacian amplitude (Manahilov et al., 1992; Srebro, 1985). In other words, the Laplacian operator acts as a spatial filter (spatial resolution is about 1.5 cm) which emphasises local sources and reduces the contribution of distant sources. Therefore, our results indicates a dominant current source located in the occipital cortical area which could be approximated by a radial dipole. The electrical activity of such a radial dipole-like source could be recorded efficiently by means of a 3-point Laplacian operator centred on Oz [Eq. (1)]. Indeed, the Laplacian responses to contrast modulations (Fig. 3a and b, right traces) contain a clearly defined negative component of the same latency as the corresponding VEP component.

The VEPs recorded at Oz to luminance gratings of 0.5 cpd contained the early positive component 1P1 (the prefix “1” represents first-order stimuli) whose peak latency was 119 ms (Fig. 3c, left trace). Gratings of 4 cpd

evoked an early negative component 1N1 of a latency of 87 ms (Fig. 3d, left trace). The generators of these components produced scalp electrical fields whose extreme values were recorded around Oz (Fig. 3c and d, left maps). The Laplacian maps showed more localized distributions of positivity for 0.5 cpd (Fig. 3c, right maps) and negativity for 4 cpd (Fig. 3d, right maps). These results indicate that the generators of the early components of the VEPs to luminance gratings could be approximated by radial electrical dipoles positioned in the medial occipital cortex. The Laplacian responses calculated by Eq. (1) enhanced the positive component of the VEPs to 0.5-cpd luminance gratings (Fig. 3c, right trace) and the negative component of the VEPs to 4-cpd luminance gratings (Fig. 3d, right trace).

3.2.1.2. Later components. The early components of the VEPs to gratings and contrast modulations described above were followed by later negative components. The later component 2N2 of the VEPs to contrast modulations of 0.5 and 4 cpd produced latency values of 336 and 310, respectively (Fig. 4a, and b, left traces). Luminance gratings evoked a late component 1N2 with a latency of 160 ms (0.5 cpd) and 180 ms (4 cpd) (Fig. 4c and d, left traces). A common characteristic of the later negative components elicited by both luminance- and contrast modulations is that their voltage scalp distributions (Fig. 4a–d, left maps) are wider than those to the corresponding early components, covering occipital, temporal and parietal scalp areas. In contrast to the Laplacian maps of the early components, the Laplacian maps of the later components (Fig. 4a–d, right maps)

did not show a restricted area of electrical current in the occipital region. Rather, the Laplacian maps of the later components revealed current sinks and sources in the temporal and parietal scalp areas. This pattern of results is consistent with complex electrical generators which may be dominant in extrastriate cortical areas. Furthermore, the Laplacian responses recorded by a 3-point Laplacian operator centred on Oz did not contain pronounced late components (Fig. 4a–d, right traces).

These data show that luminance and contrast modulations evoke VEPs whose early components are generated by neuronal structures which could be approximated by radial dipoles located within medial occipital cortex. These components were recorded more efficiently by a 3-point Laplacian operator centred on Oz as compared to a monopolar Oz derivation. Therefore, we used this Laplacian operator to investigate the characteristics of the early component of the responses to luminance and contrast modulations.

3.2.2. Laplacian responses to first- and second-order patterns

Fig. 5 illustrates the variability of the Laplacian responses to first- and second-order modulations across the tested subjects. The early negative component 2N1 elicited by contrast modulations of 0.5 and 4 cpd was the most pronounced and repeatable across the seven subjects (Fig. 5a). The mean Laplacian responses (Fig. 5a, thick trace) contained mainly the early 2N1 component (latency of about 200 ms), although the later negative component 2N2 could be identified in the Laplacian responses of some subjects.

The early components of the Laplacian responses to luminance gratings of 0.5 cpd (1P1) and 4 cpd (1N1) were well defined and repeatable across the four tested subjects (Fig. 5b). The mean Laplacian responses contained mainly the early components whose latencies were about 120 ms for gratings of 0.5 cpd and 100 ms for gratings of 4 cpd. One might suggest that the responses to contrast modulations are delayed as compared to those evoked by luminance gratings due to masking effects of the noise carrier used to construct the second-order patterns. In order to test this suggestion, we recorded Laplacian responses to gratings embedded in dynamic noise (Fig. 5c). The responses to noiseless gratings (Fig. 5b) and gratings in noise (Fig. 5c) had similar waveforms and latencies, although the presence of noise resulted in reduced amplitudes.

3.2.3. Effects of modulation depth

Another factor which influences VEPs is modulation depth. The mean amplitude of the early components to luminance gratings of 0.5 cpd (1P1) and 4 cpd (1N1) increased as grating contrast increased (Fig. 6a and b, circles). The masking effect of noise on the amplitude of these components was stronger for luminance gratings

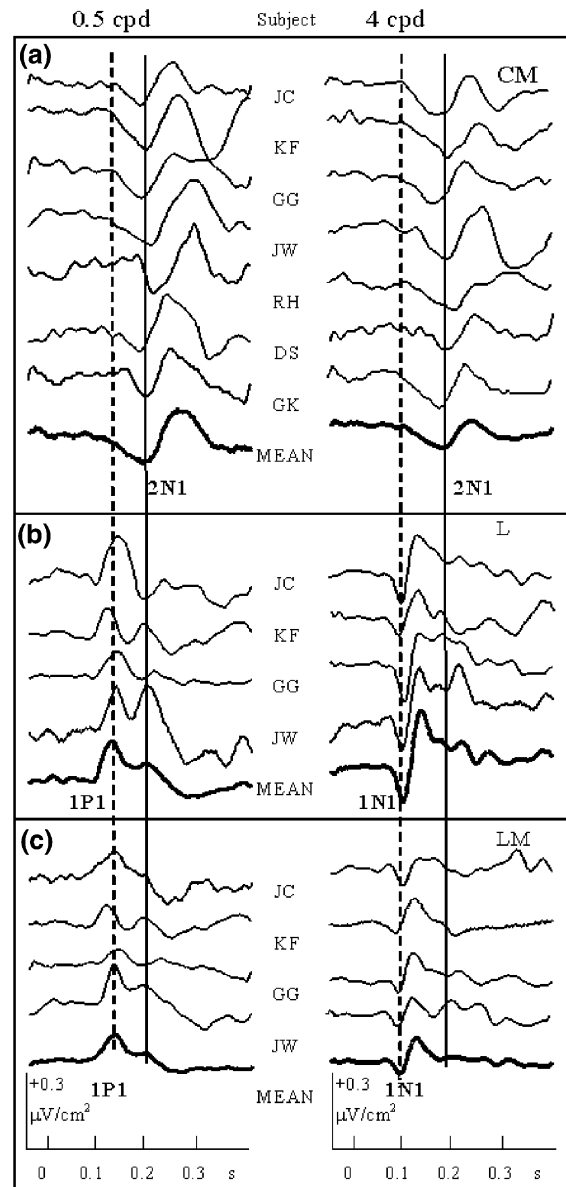


Fig. 5. Laplacian responses centred on Oz recorded from the tested subjects: (a) Laplacian responses to contrast modulations of dynamic noise (contrast 0.9) of 0.5 cpd (left traces) and 4 cpd (right traces) for seven subjects; (b) Laplacian responses to gratings (contrast 0.1) of 0.5 cpd (left traces) and 4 cpd (right traces) for four subjects; (c) Laplacian responses to gratings embedded in dynamic noise of 0.5 cpd (left traces; contrast 0.1) and 4 cpd (right traces; contrast 0.13) for four subjects. The thick traces show the mean responses averaged across the tested subjects.

of 4 cpd than for luminance gratings of 0.5 cpd (Fig. 6a and b, diamonds). The mean amplitude of the 2N1 component of the responses to contrast modulations of 0.5 and 4 cpd also increased as a function of modulation depth (Fig. 6a and b, filled squares). The mean latencies of the 1P1 (Fig. 6c, circles) and 1N1 (Fig. 6d, circles) components of the responses to luminance gratings of 0.5 and 4 cpd, respectively, decreased as a function of grating contrast, especially at low contrast levels.

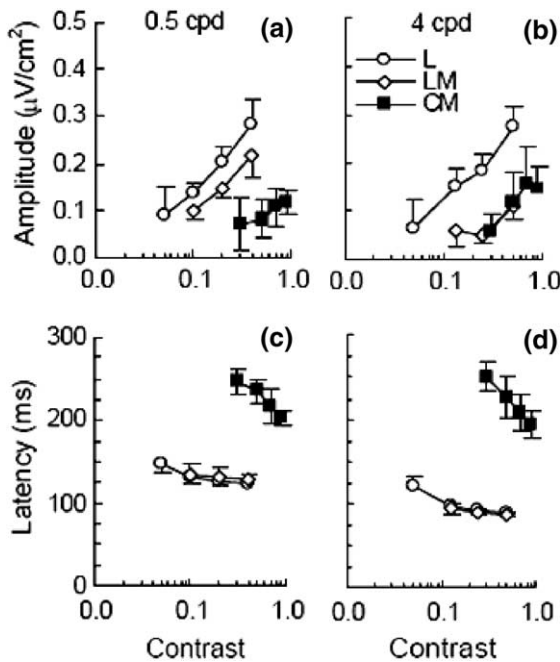


Fig. 6. Mean Laplacian amplitude centred on Oz (a and b) and latency (c and d) of the components 1P1 and 1N1 elicited by luminance modulations and 2N1 in response to contrast modulations as a function of modulation depth. Left panels: data for stimuli of 0.5 cpd; right panels: data for stimuli of 4 cpd. Error bars indicate 95% confidence interval. (a) Data from seven subjects. (b and c) Data from four subjects.

The latencies of the responses to luminance gratings in the absence and presence of dynamic noise (Fig. 6c and d, diamonds) were not significantly different (t -test, $p > 0.15$). The 2N1 components of the responses to both 0.5- and 4-cpd contrast modulations exhibited much longer latencies and steeper functions of modulation depth than the early components of the responses to luminance modulated stimuli (Fig. 6c and d, filled squares).

For modulation signals of 0.5 cpd, the comparison between the latency of the 1P1 component of the responses to luminance gratings embedded in noise (contrast 0.1) and the latency of the 2N1 component of the responses to contrast modulations (contrast 0.9) were significantly different (t -test, $p < 0.001$). Luminance (contrast 0.13) and contrast modulations (contrast 0.9) of 4 cpd evoked responses whose early negative components also had significantly different latencies (t -test, $p < 0.001$). These comparisons were made for contrast levels four times above the thresholds for detection of the luminance and contrast modulations as explained in the Results section 3.1. The results clearly show that the responses to contrast modulations are slower than those to luminance modulations and this difference cannot be accounted for by differences in the sensitivity to these stimuli.

In summary, the early components of the Laplacian responses to contrast modulated patterns peaked

at around 200 ms and were negative for low and higher spatial frequencies. The Laplacian responses to luminance modulations produced early components with peaks at 130 ms and 100 ms for 0.5 cpd and 4 cpd respectively. The response to 0.5 cpd was positive, while that for 4 cpd was negative.

3.3. Experiment 2

In Experiment 1, the voltage and Laplacian maps of the early components evoked by luminance and contrast modulations indicated that the generators of these components might be approximated by a radial dipole located in the occipital cortical area. Experiment 2 was aimed at testing the suggestion that the sources of the early components evoked by contrast modulations have a striate origin.

The cruciform model of the primary visual cortex (Jeffreys & Axford, 1972; Spekreijse et al., 1977) describes how the projections of upper and lower visual fields face one another across the calcarine fissure and parts of the left and right visual fields face each other across the midline fissure. According to this model, a stimulus presented in the visual-field periphery evokes activity which could be approximated by a tangential dipole. The spatial distribution on the scalp of electrical signals generated to a tangential source contains areas of positive and negative amplitudes which are located laterally in respect to the dipole position (see illustrations in Manahilov et al., 1992). Therefore, stimuli displayed in the upper/lower or left/right areas of the visual field evoke activity which produces electrical responses of opposite polarity. Thus, polarity reversal of the early components evoked by gratings indicates that the generators of these components are located in the striate cortex.

In order to assess whether the early components evoked by contrast modulated patterns had a striate origin, we carried out multiple-channel recording of VEPs to contrast modulations which were presented in the upper, lower, left or right parts of the visual field. Fig. 7 represents VEP traces of three subjects to contrast modulations of 0.5 cpd (Fig. 7a) and 4 cpd (Fig. 7b) recorded from the lateral electrodes P5 and P6 and the midline electrodes CPz and Iz (the electrode locations are marked by squares in the inset). At least 200 sweeps were recorded for each condition in order to produce reliable VEPs. The stimulation of the upper field evoked positive responses at the CPz position and negative responses at the Iz position (Fig. 7a and b, upper panels). There was polarity inversion of these responses, when the stimuli were presented in the lower field (Fig. 7a and b, lower panels). Stimuli displayed in the left field elicited positive and negative responses at the positions P5 and P6, respectively (Fig. 7a and b, left panels). The transposition of the stimuli from the left to the right

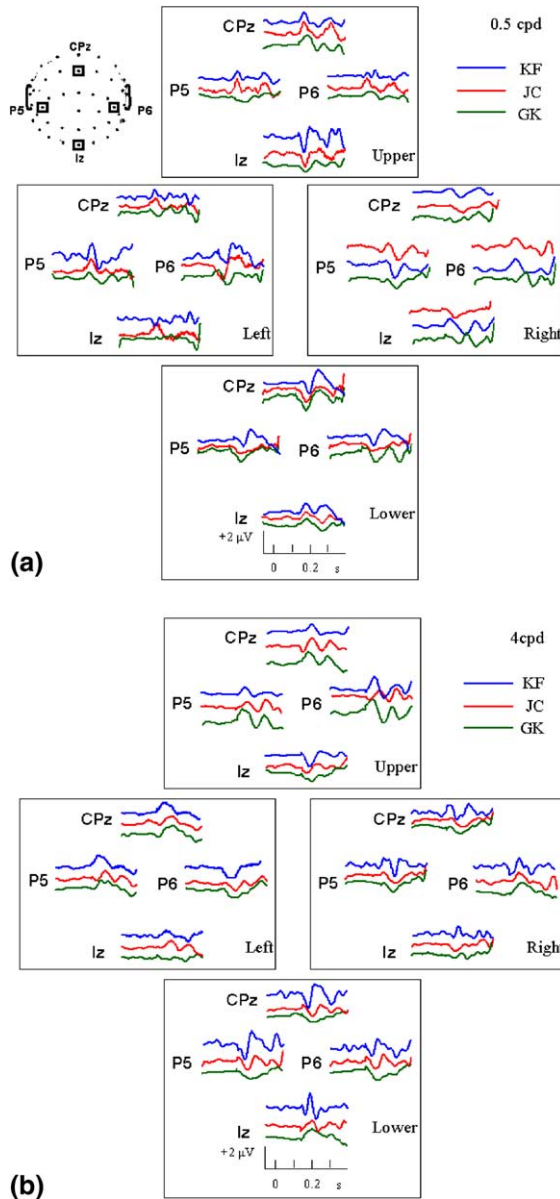


Fig. 7. VEPs for three subjects elicited by half-field contrast modulations. The VEPs were recorded from lateral electrodes P5 and P6 and midline electrodes CPz and Iz whose locations are shown in inset. (a) data for modulation spatial frequency of 0.5 cpd; (b) data for modulation spatial frequency of 4 cpd.

field resulted in polarity inversion (Fig. 7a and b, right panels).

Fig. 8 shows voltage maps of the responses to contrast modulations of 0.5 (Fig. 8a) and 4 cpd (Fig. 8b) which were averaged across the three tested subjects within the 150–235 ms interval corresponding to the most prominent components of the Laplacian responses. For lower-field stimuli (Fig. 8a and b, lower maps), the responses were negative at the central scalp and positive at the lower occipital sites. Upper-field stimuli evoked responses with reversed polarities: a negative polarity at the lower occipital sites and a po-

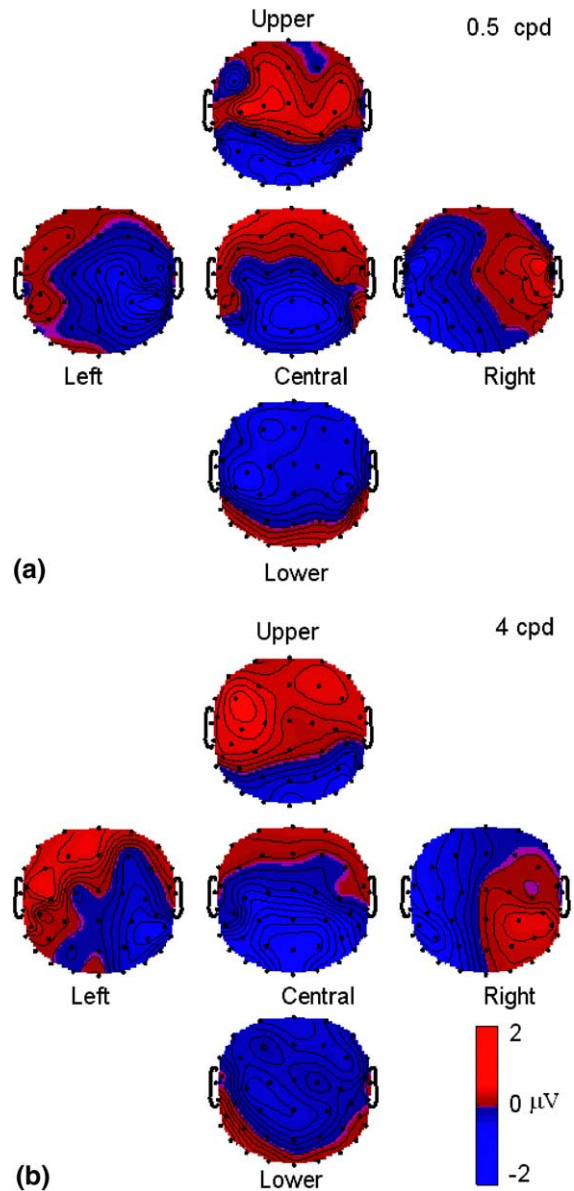


Fig. 8. Spline-interpolated voltage maps of the component 2N1 elicited by contrast modulations of 0.5 cpd (a) and 4 cpd (b) and averaged within the latency range 150–235 ms. The stimuli are presented in the central, upper, lower, left or right visual fields. Oz and Cz locations are indicated. Averaged data of three subjects.

sitive broad distribution across parietal-central-temporal areas (Fig. 8a and b, upper maps). The stimulation of the left and right fields elicited negative responses in the temporal site contralateral to the stimulus position while the responses recorded in the ipsilateral temporal sites were positive (Fig. 8a and b, left and right maps).

In summary, these results show a clear reversal of response polarity to contrast modulations of 0.5 and 4 cpd at stimulation of upper/lower and left/right parts of the visual field which suggests that the component 2N1 has a striate origin.

3.4. Control experiment

Stationary modulations of noise contrast contain second-order information which is determined by the modulation signal. In addition, however, the onset of such stimuli is accompanied by luminance changes. These first-order artefacts are luminance patches of various sizes and amplitudes which are determined by the stochastic properties of the noise carrier (Smith & Ledgeway, 1997). Samples of 2D binary noise which are constructed by randomly distributed light and dark pixels, are likely to contain local regions of imbalance of dark and light pixels. Therefore, contrast modulations may evoke VEP components which reflect activity of both first- and second-order mechanisms.

In order to test this possibility, we recorded VEPs to contrast modulations of static noise whose modulation depth (0.9) was approximately four times above the detection threshold contrast. The waveform of the Laplacian responses to contrast modulations of 0.5 and 4 cpd for most of the six tested subjects contained mainly two negative components (Fig. 9). The latencies of the first negative component were similar across the tested subjects which resulted in the presence of this component in the mean Laplacian responses (Fig. 9). The mean latency and 95% confidence interval of the first component was 117 ± 6 ms for contrast modulations of 0.5 cpd and 121 ± 12 ms for contrast modulations of 4 cpd. The latencies of the later negative component varied in a wider range and it was not present in the mean Laplacian responses. This component, however, could be identified in the individual traces and its mean latency and 95% confidence interval was 196 ± 17 ms (0.5-cpd contrast modulations) and

207 ± 23 ms (4-cpd contrast modulations). For each modulation spatial frequency the latencies of the first and second negative components were significantly different (*t*-test, $p < 0.001$).

Contrast modulations of static noise are likely to contain local luminance artefacts. Such luminance patches would have relatively higher spatial frequencies. Studies have shown that gratings of higher spatial frequencies evoke an early negative component whose latency increases as spatial frequency increases (Parker & Salzen, 1977; Vassilev & Strashimirov, 1979; Vassilev, Manahilov, & Mitov, 1983). Therefore, the first negative component might reflect activity evoked by local luminance artefacts of contrast modulations of static noise. The later negative component has a latency which is similar to that of the 2N1 component of the Laplacian responses to contrast modulations of dynamic noise, which indicates that this component might be generated by structures processing second-order information.

4. Discussion

VEPs elicited by luminance patterns have been used to study the organization of the human visual system. In accordance with previous studies of VEPs to luminance gratings (Manahilov & Vassilev, 1986; Parker & Salzen, 1977; Parker et al., 1982a, Parker, Salzen, & Lishman, 1982b; Plant, Zimmern, & Durden, 1983; Vassilev et al., 1983) we found that with central fixation, the early component of the Laplacian responses to the onset of 0.5-cpd luminance modulations had a positive polarity and a latency of about 130 ms, while luminance modulations of 4 cpd elicited an early negative component with a latency of about 100 ms. These VEP components were usually followed by a later negative component with a latency of around 180 ms. The early VEP components were larger at Oz than laterally, while the later negative component was more widely distributed and was dominant at the lateral electrodes. Studies of pattern adaptation effects on VEPs (Manahilov & Vassilev, 1986; Smith & Jeffreys, 1978) have found that the early components exhibited spatial-frequency selectivity, while the adaptation effects on the amplitude of the later negative component did not. Spatial-frequency selective structures are assumed to exist in the primary visual cortex which suggests that the generators of the early components are located within the striate cortex. Using quadrant stimulation, Parker et al. (1982a) reported polarity reversal of the early component of VEPs elicited by gratings of 3–8 cpd. Applying the cruciform model of generator orientation in the human striate cortex (Jeffreys & Axford, 1972; Spekreijse et al., 1977), they suggested that the early component recorded at medium spatial frequencies originates from the striate cortex. The later negative component did show polarity

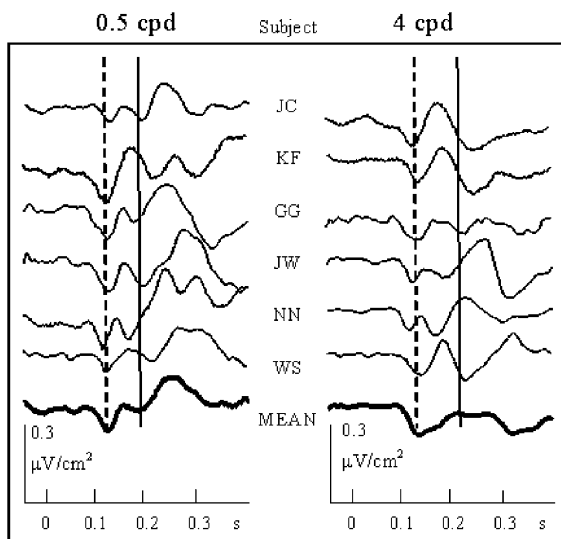


Fig. 9. Laplacian responses to contrast modulations of static noise (contrast 0.9) of 0.5 cpd (left traces) and 4 cpd (right traces). The thick traces show the mean responses averaged across the six tested subjects.

reversal with lower and upper field stimulation, but did not show polarity inversion when the stimulus was translated across the midline as predicted by the cruciform model of the striate generator. A topographical analysis of scalp recorded VEPs has confirmed that the early component (50–80 ms) elicited by a small checkerboard stimulus changes its polarity and topography systematically as a function of stimulus position in a manner consistent with the retinotopic organization of the striate cortex (Clark, Fan, & Hillyard, 1995). Clark et al. (1995) noted that such effects of stimulus location on the polarity of the VEPs would not be observed for VEPs generated in other visual areas since extrastriate areas do not have the special retinotopic organization of the calcarine cortex, although there may be some degree of polarity reversal of the responses of neural structures in V2 and V3 for upper versus lower field stimuli. These data suggest that the generators of the early VEP component might reflect activities mainly of striate neurons which could be associated with the pathway processing first-order luminance information.

The present results have shown that the first prominent component of the responses to contrast modulations of 0.5 and 4 cpd has a negative polarity and a latency of about 200 ms which is significantly longer than that of the early components of the responses to luminance modulations. Although we found a latency difference between the responses to both patterns, the potential and Laplacian maps of the early components of the responses to luminance- and contrast-modulated patterns had similar scalp distributions suggesting a dominant current source located in the occipital cortical area. Additionally, the polarity reversal of the responses to contrast modulations presented in upper/lower and left/right parts of the visual field indicates that the first prominent component of these responses is likely to be generated within the primary visual cortex although generators located in adjacent extrastriate cortical areas (V2, V3) might contribute to the responses elicited by contrast-modulated patterns.

According to the “linear-rectifier-linear” model, the pathway processing second-order information consists of first-stage linear filters followed by a non-linearity and second-stage linear filters. One might suggest that the responses to contrast modulations might be elicited by activity of the second-stage linear filters which extract the modulating signals from the output of the non-linearity. Wilson et al. (1992), Yo and Wilson (1992) and Ellemberg et al. (2003) have suggested that contrast modulations require a longer processing time than those to luminance modulations due to the additional stages which are involved in the processing of second-order information. On the other hand, research has suggested that the second-stage linear filters utilise outputs of first-stage filters tuned to carrier spatial frequencies which are higher than the modulation spatial frequency (Schofield

& Georgeson, 2000; Sutter, Sperling, & Chubb, 1995). Studies have shown that the latency of VEPs to gratings increases as the grating spatial frequency increases (Parker & Salzen, 1977; Vassilev & Strashimirov, 1979; Vassilev et al., 1983). Therefore, the longer latency of the responses to contrast modulations could be accounted for by two factors: the slower first-stage linear filters and the additional processing stages of the second-order pathway.

It should be noted that the “linear-rectifier-linear” model does not necessarily require that different neuronal structures underlie each stage of the second-order pathway. It is possible that the same neuronal structure performs different functions (Zhou & Baker, 1993). Visual information processing also includes various streams of neuronal activity that could be involved in the analysis of second-order patterns. Research has shown that visual information is processed by a cascade of feedforward connections from low-level to high-level areas of the visual cortical hierarchy (Felleman & Van Essen, 1991). This stream of activation can be modified by input from horizontal within-area connections and feedback from higher areas (for a review see Lamme & Roelfsema, 2000). One may speculate that the longer latency responses to contrast modulations may also be due to delays in second-stage linear striate neurons having inputs from extrastriate neurons via feedback connections. This suggestion is in line with the integrated model of visual processing (Bullier, 2001) which assumes that first-order stimuli rapidly activate V1 and V2 neurons while more complex second-order patterns require additional computations in higher order cortical areas which are integrated via feedback connections by V1 and V2 neurons acting as “active blackboards”.

Previous studies have recorded texture-segregation VEPs to patterns defined by second-order features such as orientation of line elements (Bach & Meigen, 1992, 1998–1999; Lamme et al., 1992), spatial frequency (Bach et al., 2000) and motion (Lamme et al., 1994). Lamme et al. (1992, 1994) employed equivalent dipole source localization methods to the scalp recorded responses in humans and current source density analysis to the intra-cortically recorded responses in awake monkey and found that responses to texture segregation are generated by structures in the primary visual cortex. Fahle, Quenzer, Braun, and Spang (2003) have also shown that the occipital cortex can perform a figure-ground discrimination using image attributes such as luminance, colour, motion direction, stereoscopic depth, and line orientation.

In these studies, the texture-specific VEP component was extracted by calculating the difference between the responses to the onset of a global modulated carrier and the responses to the onset of a homogeneous non-modulated carrier. We recorded the VEP component elicited by second-order patterns using a different

paradigm. The onset of contrast modulations of visual noise was preceded by a blank interval containing a non-modulated carrier. This stimulus contains a second-order signal at the modulation frequency as well as first-order localized luminance patches of various sizes and contrast levels due to imbalance of dark and light noise (Smith & Ledgeway, 1997). The control experiment has shown that responses to contrast modulations of static noise contain an early component which may be generated by first-order pattern-specific mechanisms sensitive to luminance artefacts. When the carrier is dynamic noise, the noise samples are updated with a high refresh rate (60 Hz). The luminance artefacts in each modulated noise sample are randomly distributed across the stimulation field which does not provide conditions for activation of luminance selective structures through temporal summation. Additionally, the dynamic noise has rich spatial- and temporal-frequency spectra and stimulates the majority of cells which respond to luminance patterns. These masking effects reduce the sensitivity of luminance-specific structures to luminance artefacts. Thus, we suggest that the VEPs to contrast modulations of dynamic noise could be regarded as free of significant contributions due to luminance artefacts.

The present results agree with those of Ellemberg et al. (2003), who found that the pattern-specific component of VEPs to drifting contrast modulations had longer latencies than those elicited by drifting luminance modulations. On the other hand, some differences between the results of these studies should be noted. Ellemberg et al. (2003) showed that the VEPs evoked by both drifting luminance and contrast modulations of 1 cpd contained early positive pattern-specific components and later negative motion-specific components. Our stationary luminance modulations of a similar spatial frequency (0.5 cpd) evoked responses which contained an early positive component while the early component due to contrast modulations of 0.5 cpd had a longer latency, but a negative polarity. One might suggest that the later negative component of VEPs to drifting contrast modulations which has been associated with a motion processing mechanism (Ellemberg et al., 2003), may also have contributions from second-order pattern-specific mechanisms. In addition, Ellemberg et al. (2003) used static noise as a carrier. Our control experiment has shown that responses to contrast modulations of static noise can consist of contributions from first-order pattern-specific mechanisms evoked by luminance artefacts.

In summary, our results have shown that the responses to contrast modulations of 0.5 and 4 cpd have longer latencies than those to luminance modulations. The topographic analysis of scalp recorded VEPs to central and half-field stimulation with contrast modulations of dynamic noise have suggested that the responses to contrast modulated patterns are likely to be elicited by

the primary visual cortex which may have inputs from extrastriate neurons via feedback connections.

Acknowledgement

This research was supported by a grant from the Biotechnology and Biological Sciences Research Council, UK (223/S13702).

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