PERGAMON

Vision Research 39 (1999) 2975–2985

Vision Research

www.elsevier.com/locate/visres

Section 1

Electrophysiological evidence for an early attentional mechanism in visual processing in humans

Francesco Di Russo [a], Donatella Spinelli [a,b,*]

[a] *Department of Psychology, Università di Roma "La Sapienza", via dei Marsi 78, 00185 Rome, Italy*
[b] *Research Center, IRCCS Ospedale S. Lucia, Rome, Italy*

Received 11 June 1998; received in revised form 28 October 1998

Abstract

The effect of sustained spatial attention on a task-irrelevant grating displayed in the left visual field was studied by steady-state and transient visual evoked potentials (VEP). For the steady-state experiment, the task irrelevant grating was phase-reversed at different temporal frequencies. In the transient experiment the grating was reversed abruptly at low temporal frequency. In both conditions a target requiring visual attention was presented either in the left or in the right visual field, directing attention either to the left or to the right. VEPs amplitude enhancement by attention was observed on steady-state VEPs and on P100 and N140 transient VEPs components, confirming previous observations. Moreover, VEPs in the attended condition had shorter latency than VEPs in the unattended condition. The difference was about 15 ms with steady-state; with transient recording the lag was 7 ms for N60 and 10 ms for P100. The latency change of the N60 component, suggests that the modulation of attention on visual processing might be earlier than previously thought. A control experiment to assess the influence of eye movements on the test was also performed.

Keywords: Attention; Visual evoked potential; Amplitude; Latency

1. Introduction

As Helmoltz noted a century ago, if visual attention is directed to a location without moving the eyes (covert attention), perception in that region is enhanced. Facilitation due to spatial attention is often measured by reaction times, that are shorter to stimuli located in the attended position of the visual field compared with the unattended one (Posner, 1980). However, a limit to this approach is that motor and sensory components are not dissociated. More relevant for the present research are studies examining the perceptual component of covert attention. Attention produces an illusory temporal order perception. Two simultaneous stimuli are perceived as asynchronous, the spatially cued one being processed faster. The size of this effect depends on the delay between the cue and the test; when the delay is long, so attention is sustained, the size is about 10–15 ms (Hikosaka, Miyauchi & Shimojo, 1993).

Other experiments have demonstrated improvement in detection (e.g. Bashinski & Bacharach, 1980) and discrimination (e.g. Nakayama & Mackeben, 1989) of a peripheral stimulus located in an attended portion of the visual field. Overall, these psychophysical results are in agreement with the idea that sustained attention acts on the speed and the quality of visual processing.

An important contribution to the study of attention has been made by electrophysiological studies, which make possible the measurement of the time-course of brain activity. By recording evoked potentials (EPs) to auditory (e.g. Woldorff & Hillyard, 1991) and visual (Luck, Fan & Hillyard, 1993) modalities it was shown that the facilitation due to spatial attention takes place at an early stage of processing. This is supported by the increase of early (N100 and P20–50 ms) EP components to attended stimuli in the auditory modality

* Corresponding author. Fax: +39-6-4451667.
E-mail address: dspinelli@axrma.uniroma1.it (D. Spinelli)

0042-6989/99/$ - see front matter
PII: S0042-6989(99)00031-0

(Woldorff, Hansen & Hillyard, 1987); for a different interpretation, see Näätänen, 1990) and by the enhancement of the early (P100, N140) EP components in the visual modality. The enhancement was only in amplitude, with no effect on the latency of the response in either modality (as summarised by Hillyard, Mangun, Woldorff & Luck, 1995, p. 669). Overall, data support the hypothesis that attention acts as a sensory gain control mechanism, modulating the flow of information differentially between attended and unattended regions (for a review, see Hillyard et al., 1995). Confirming previous suggestions (Mangun & Hillyard, 1990), a study based on the combined P100 data and PET analysis showed that for visual attention this modulation takes place at the level of the extra-striate cortex (Heinze, Mangun, Burchert, Hinrichs, Scholz, Munte et al., 1994).

The present work focuses on the effect of attention on the latency of visual evoked potentials (VEP). Attention is a system for providing priority for motor acts, consciousness and memory (Posner, 1995). Priority for action towards a target may be based, at least in part, on priority at the sensory level (Duncan & Humphreys, 1989). Priority at the sensory level may be mediated by variation of the processing speed of inputs from cued locations. Our working hypothesis is that attention has an effect on the speed of sensory processing.

A particularly sensitive method for measuring VEP latency is the steady-state VEP to stimuli of varying temporal frequency (Regan, 1966; Spekreijse, Estevez & Reits, 1977; Porciatti, Burr, Morrone & Fiorentini, 1992). For instance, this technique has proven useful in detecting the increase in VEPs latencies in brain damaged patients with hemi-neglect. These patients suffer from an attention defect limited to stimuli in the left portion of space; the VEPs latencies to stimuli in the left neglected hemifield were longer than those to stimuli in the right hemifield. This observation indicates that this spatial attention deficit is associated with a delay in the early sensory processing (Spinelli, Burr & Morrone, 1994; Spinelli & Di Russo, 1996).

Few studies on attention with steady-state VEPs have been reported. The few that exist focus on the amplitude of responses and their results are contradictory, probably due to differences in the experimental procedures. No enhancement was observed by Silberstein, Schier, Ciorciari, Pipingas, Wood and Simpson (1995) while Morgan, Hansen and Hillyard (1996) obtained a very strong (up to 100%) enhancement for task-irrelevant background phase-reversed stimuli in the attended location. In the present research, we confirm the latter finding, and also observed a large effect of attention on VEP latency.

One limit of the steady-state technique is that it prevents the labelling of different components, typical of transient EP recording and associated with different sources. For this reason, in a second experiment we analysed the effect of attention on the various components recorded by transient VEP (N60, P100, N140, P200). This experiment gave further information about the level at which the effect of attention on latency and amplitude takes place.

2. Material and methods

In both experiments the VEPs were recorded in response to a grating (a task-irrelevant background) continuously displayed in the left hemifield. The target was a small spot that changed colour superimposed on the grating in the attended condition or on a Gary background in the right hemifield in the unattended condition. The subject was instructed to covertly orient his/her attention towards the side where the spot would be displayed. Thus, the experiment investigated the effect of attention tonically maintained at the same spatial location.

2.1. Subjects

Eleven subjects (four males and seven females; mean age 33 years, S.D. 11.9) participated in this study; all subjects had normal or corrected to normal vision. Five of them were trained observers. All subjects were informed about the general purpose of the experiment in order to obtain the maximum reliability in the fixation task. Steady-state VEPs were recorded in five subjects, transient VEPs in six subjects.

2.2. Stimuli

The stimuli were displayed on a monitor (Barco CDCT 6551) with mean luminance of 16.5 cpd/m2 and frame rate 100 Hz. A cross in the centre of the display served as fixation point. The stimulus was a horizontal sinusoidal 1 cpd grating of 85% contrast, 11° wide and 18° high. The grating was always displayed in the left visual field (LVF).

The edge of the grating was 1.5° to the left of the fixation point. An unpatterned area of the same mean luminance as the LVF stimulus was displayed in the right visual field (RVF). In the steady-state VEP condition, the grating contrast was reversed sinusoidally at nine temporal frequencies (5, 5.5, 6, 6.5, 7, 7.5, 8, 8.5, 9 Hz). In the transient VEP condition, the grating contrast was squarewave reversed at a low temporal frequency (varying in random way between 0.5 and 0.8 Hz). The target stimulus, used to draw attention, was a 2° spot located 7° to the left or to the right of the fixation point. The colour of the spot turned from green to red at a random rate (once every 2.5–5.5 sec).

2.3. Procedure

The subject, seated in a dimly lit room 60 cm from the screen, was instructed to keep his eyes on the fixation point. The subject's task was to direct attention to the target spot and count how many times it turned red. When required, the subject had to report the number of alternations. Two experimental conditions were studied. (1) Attended condition: the target was located in the LVF, superimposed on the grating. (2) Unattended condition: the target was located in the RVF. Thus, in Condition 1 the potentials were evoked by the grating displayed in the attended hemifield; in Condition 2 the potentials were evoked by the same stimulus displayed in the same hemifield, but in this case attention was oriented toward the other side. Each EP was evoked by 150–200 stimulus repetitions. The two conditions were presented in two blocks separated by a two-minute interval. Shorter interval (30 s) were given at the end of each temporal frequency when steady-state technique was used. The duration of the sessions were about 15 min and about 5 min for steady state and transient recording, respectively. Each subject was tested in one attended and one unattended condition. The order of condition (attended and unattended) was balanced across subjects.

2.4. VEPs recording and data analysis

2.4.1. Steady-state VEPs

VEPs were recorded from scalp electrodes, Oz active with Cz reference and Pz ground. Signals were amplified (50 000 fold), band-pass filtered (1–100 Hz) and digitised at 64 points/period. The steady-state VEP waveform is roughly sinusoidal and is well described by the amplitude and phase of the second harmonic Fourier component (Campbel & Maffei, 1970). Phase changes with temporal frequency and apparent latency may be derived by measuring the phase as a function of temporal frequency and estimating the slope of the curve (Regan, 1966; Spekreijse et al., 1977). The phase of the second harmonic is plotted in π radians as a function of temporal frequency under the assumption that phase advances or retard regularly with temporal frequency. Thus, multiple of 2π radians are added or subtracted to the raw data, in order to produce the maximum orderliness. The method used was developed by Burr and Morrone in various studies (e.g. Porciatti et al., 1992; Morrone, Burr & Fiorentini, 1993; Morrone, Fiorentini & Burr, 1996). The computer performed on-line Fourier analysis to calculate the amplitude and the phase of the second harmonic component. At the same time, the computer averaged the electrical signals at a temporal frequency near that of the stimulus but not synchronously with it. This was taken as an index of noise and artefacts, to assess VEP reliability. For each packet of 20 sums (20 periods of stimulus presentation) the signal-to-noise ratio was calculated. As an independent measure of variability the standard error of the amplitude and phase was calculated from the two-dimensional scatter in amplitude and phase of the individual 20-sum packet. The latency was estimated from the slope of the regression line of phases as a function of temporal frequency. The slope was calculated by least-squares fit, after weighting each data point by its signal-to-noise ratio.

VEP amplitudes were evaluated with a one-between two-within factors ANOVA; order of conditions (two levels), attention (two levels: attended and unattended) and temporal frequency (nine levels 5–9 Hz). Latencies were evaluated with a one-repeated factor ANOVA; attention (two levels: attended and unattended). The post-hoc comparisons were based on Tukey's Honest Difference test. The overall alpha value was fixed at 0.05.

2.4.2. Transient VEPs

Digital EEG was recorded on-line. EEG was sampled continuously at 2 ms using NeuroScan Inc. software (SCAN version 4.0) on a Pentium PC. Twenty scalp electrodes were used according to the 10–20 International System. The EEG was amplified 50 000 fold and filtered (DC-70 Hz). The EOG was amplified 10 000 and filtered (DC-70 Hz). Electrodes were referred to the linked mastoids; the ground was on FPz. Epochs of 800 ms, including 200 ms pre-stimulus interval, were extracted from the EEG. Epochs corresponding to EOG amplitudes greater than 80 μV and EEG amplitudes greater than 50 μV were automatically rejected. This threshold for EOG provided elimination of eye movement of about 3°. Further EOG analysis was performed off-line and portions of VEP recording associated with eye movements of about 1° were rejected (about 2%). Amplitudes (relative to pre-stimulus baseline), and peak latencies of major VEP components were calculated for each subject in the following time window: N60 (35–80 ms), P100 (70–140 ms), N140 (130–230 ms), P200 (160–260 ms). Amplitudes and latencies relative to each window were separately analysed with eight, one-between two-within factors ANOVAs. Factors were order of conditions (two levels), attention (two levels: attended and unattended) and electrode position (eight levels: Oz, O1, O2, Pz, P3, P4, T5 and T6). The post-hoc comparisons, overall alpha value and covariate factor as above.

3. Results

In all cases the number of target reversals was reported correctly by the subjects. This confirmed that subjects attention was effectively directed toward the target. All subjects reported occasional lapses of gaze. However, in general, they felt confident in following the instructions.

3.1. Steady-state VEP

Recordings obtained from one subject at all temporal frequencies in the two conditions (attended/unattended) are presented in Fig. 1. In the lower right part of the figure, phase data are plotted as a function of temporal frequency and latencies are derived for the two conditions. Inspection of the figure shows the difference in amplitude of evoked responses in the two conditions (note increments of about 100% in the 7–8 Hz range). Amplitude data are reported in the upper right part of the figure. VEP reliability can be appreciated by a comparison with the noise levels simultaneously recorded in each condition.

3.1.1. Amplitudes

The VEP amplitudes averaged across subjects are reported in Fig. 2 (left part). The amplitude enhancement by attention is evident (on the average, across temporal frequencies and subjects, the increment was 44%).

The effect of attention was significant ($F(1, 3) = 43.38$; $P < 0.025$). The effect of temporal frequency was not significant ($F(8, 24) = 1.39$; n.s.) Interaction between the two factors was significant ($F(8, 24) = 3.04$; $P < 0.05$). Post-hoc analysis showed that the effect of attention was significant at all frequencies above 5.5 Hz (at least $P < 0.01$) and the effect of temporal frequency was significant only in the attended condition (showing a peak in the region 6.5–8.5 Hz; $P < 0.05$).

3.1.2. Latencies

Phase data were averaged across subjects and latencies were calculated. The plots are reported in Fig. 2 (right part). A clear effect of the attention on the latency was present ($F(1, 3) = 73.84$; $P < 0.005$). Latencies in the attended condition (135 ms) were shorter than those recorded in the unattended condition (149 ms).

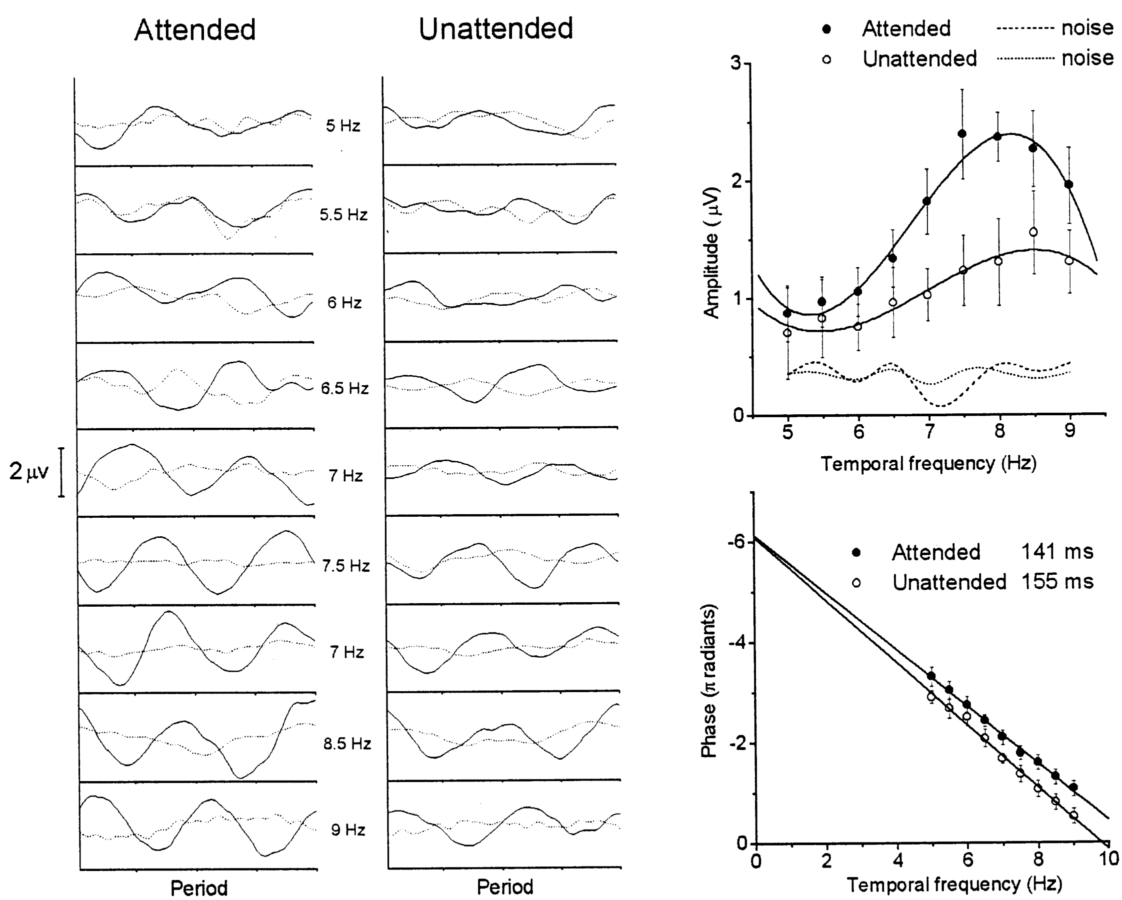

Fig. 1. Steady-state VEPs. The phase and amplitude variation of waveforms as a function of temporal frequency can be observed in the left part of the figure where the recordings obtained in one subject in the attended and unattended conditions are shown. Dotted waves report the simultaneously recorded noise signals. Stimuli were contrast-reversed at increasing temporal frequencies (5–9 Hz); responses were recorded with appropriate time analysis (from top to bottom: 200, 182, 167, 154, 143, 133, 125, 111, 118 ms). The resulting latency is shown in the lower right part of the figure. In the upper right part of the figure VEPs amplitude data and noise are reported. Bars represent the standard deviation of the amplitudes and phases of the individual 20-sums packets (for the method, see Porciatti et al., 1992).

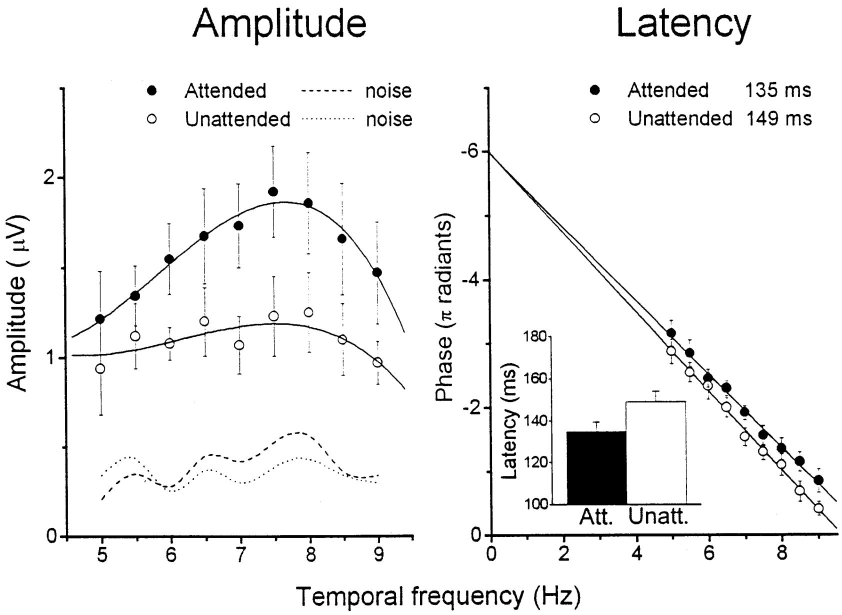

Fig. 2. Data of steady-state VEPs averaged across subjects in the two conditions. Left part of the figure: mean amplitudes and standard errors are reported as function of temporal frequency. Mean noise level in the two conditions is also reported. Right part of the figure: mean phases in π radians units are reported as a function of temporal frequency. Note the difference in phases between the two conditions. Apparent latencies are derived from the slopes of the regression lines. Mean latencies and standard errors across subjects are represented in the histogram.

3.2. Transient VEP

The grand average VEP waveforms obtained at six posterior electrodes in the two conditions (attended and unattended) are presented in Fig. 3. Four major peaks were evident in all subjects: a small negative peak around 60 ms (N60); a large positive peak around 100 ms (P100); a negative peak around 140 ms (N140) and a positive peak around 205 ms (P200). Analysis of variance was performed on eight electrodes (Oz and Pz were included).

3.2.1. Amplitudes

Mean data for N60, P100, N140 and P200 are reported in Fig. 4a. As expected, the effect of attention turned out to be significant for P100 ($F(1, 4) = 11.87$; $P < 0.025$) and N140 ($F(1, 4) = 8.19$; $P < 0.05$) components but not for N60 and P200. On the average, attention enhanced the P100 component by 70% and the N140 by more than 100%. The interaction between attention and electrodes in the two analyses was not significant, indicating that the effect of attention for these components was present at all leads.

The effects of electrode position was significant for N60 ($F(7, 28) = 3.59$; $P < 0.01$) with larger amplitudes in Oz than T5 and T6 ($P < 0.05$), for P100 ($F(7, 28) = 6.38$; $P < 0.001$) with larger amplitudes in O2 than in all other electrodes ($P < 0.025$).

3.2.2. Latencies

Mean data for N60, P100, N140 and P200 are reported in Fig. 4b. The latencies were shorter in the attended condition for N60 ($F(1, 4) = 11.28$; $P < 0.05$) and P100 ($F(1, 4) = 42.21$; $P < 0.005$). The difference between attended and unattended condition was 7 ms for N60, 10 ms for P100, 7 ms for N140 ($F(1, 4) = 4.87$; n.s.) and −5 ms for P200 ($F(1,4) = 11.98$; $P < 0.05$).

In all cases the interaction between attention and electrodes was not significant, indicating that the effect of attention was present at all leads.

The effect of electrode position was significant (at least $P < 0.05$) in all cases except for the P200. In general, the latencies were a few ms shorter at the right side leads.

3.3. Control experiments

3.3.1. Eye movements

In all studies on spatial attention, it is important to control for adequate eye fixation. Eye movements towards the attended location would vary the eccentricity of the stimulus, improving stimulus perception. Similarly, in EPs studies, it is important that the stimuli have the same retinal eccentricity in the conditions tested. If this is not so, then the attentional effect will be confused with the contribution to the EPs of different neural populations. To avoid spurious effects of eccentricity variation, eye movements were controlled in the previous experiment by the electroculogram. EOG inspection allowed the rejection of trials associated with detectable ocular deflections. However, we performed a further control of eye movements by measuring the effects on the evoked potentials due to small variations of grating eccentricity, such as those possibly produced by a small gaze shift in the direction of the grating. In this case there was no target and no covert attention task. The grating was displayed in the LVF and the subject's task was to hold his gaze on the fixation point, which was displaced towards the grating in different trials. The experiment was carried out with both steady-state and transient VEPs.

Data from the steady-state condition are reported in Fig. 5 for an individual subject (top of the figure) and summarised for three subjects (bottom). Inspection of the figure shows a clear effect of the fixation point on the amplitudes: when the gaze is shifted toward the LVF where the grating is displayed, a large amplitude enhancement is recorded. However, the latency variations were generally small in size and did not show a systematic trend. The largest decrease of the latency observed was about 6 ms, while in the same subject the effect of attention measured on the previous experiment was 14 ms.

Data from the transient condition were similar. Recordings of an individual subject are presented at the top of Fig. 6, showing a clear effect of fixation position on the amplitude of the various components. Small changes in eye positions, such as 1°, have a strong effect on the amplitude. In particular, a shift of 1.5° from the reference fixation point towards the edge of the grating has an effect on the amplitude which is about 100% for N60 and N140, 27% for P100 and 17% for P200. In this subject, the effect of eye position saturates at 0° of eccentricity for all components except P100. The latter amplitude increases linearly with gaze displacement in the entire range studied.

On the other hand, latency was less affected by eye position. The curves are rather flat and there is no

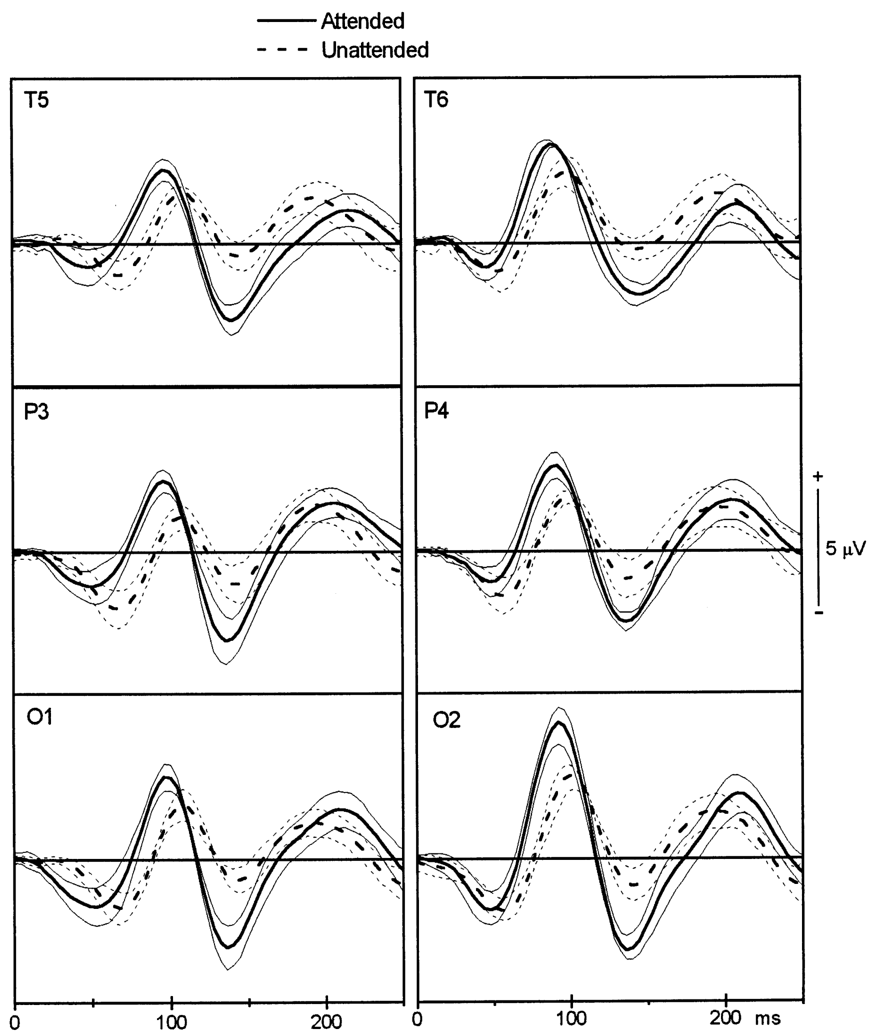

Fig. 3. Grand average of transient VEP recorded from six selected channels in the two conditions. Heavy continuous lines: Attended condition. Heavy dashed lines: unattended condition. The thin lines report the standard errors across subjects. Note that the effect of attention is present on both amplitude and latency of P100 while it is present only on the latency of N60. Data at Oz and Pz were omitted.

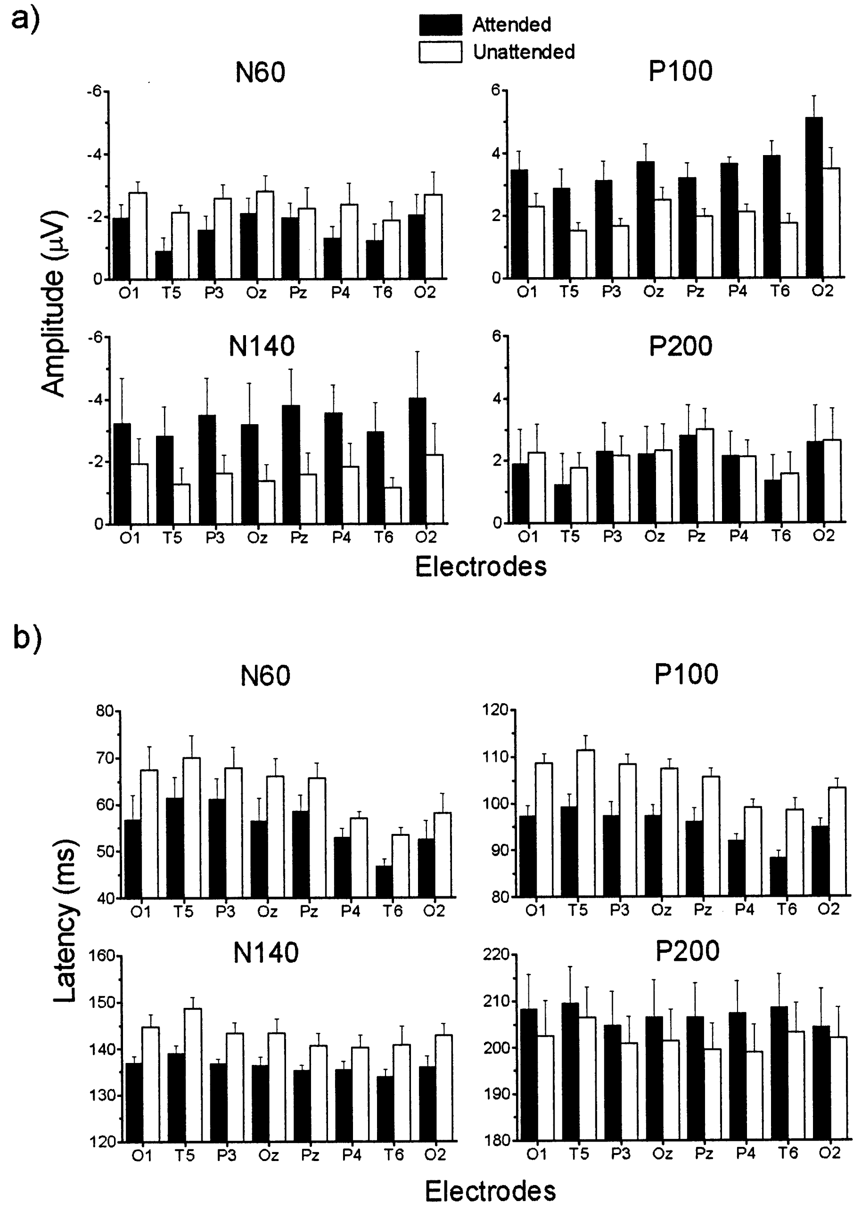

Fig. 4. (a) Mean amplitudes and standard errors (across subjects) of VEPs components at the eight selected electrodes. Black columns: attended condition; white columns: unattended condition. (b) Mean latency and standard errors. Symbols as in (a).

systematic tendency to shorten the latency when stimuli impinge on a less eccentric portion of the retina. The data of two subjects (amplitude and latency) are summarised in the lower part of Fig. 6. It may be noted that gaze manipulation enhances (in different extent) all components, but attention has no effect on the amplitude of N60.

Overall, these experiments show that small gaze-shifts towards the grating affect VEP amplitude in the same direction of attention. However, latency is less affected by this manipulation.

3.3.2. *The influence of the target stimulus on the VEP*

As described in the methods, a spot was superimposed on the grating in the attended, but not in the unattended, condition. This implies a difference between conditions also in the physical properties of the stimulus. This difference is rather small (the spot was 2°, superimposed at 7° of eccentricity on a $11 \times 18°$ grating). However, the influence of the target stimulus 'per se' on the evoked responses was measured in this experiment. In this case attention was not manipulated; VEPs were recorded in two conditions, i.e. in the presence or absence of the spot. Results are presented in Fig. 7 and show that there are no systematic differences between the two conditions either in amplitude or latency.

4. Discussion

Attention might improve performance efficiency by allocating a high proportion of resources to stimuli at the cued location. The increment of EP amplitude due to spatial attention is consistent with the action of a sensory gain control mechanism. Another, but not alternative, attentional mechanism is that of establishing a priority order in processing information (Duncan & Humphreys, 1989). In this view, a faster signal might determine the priority of sensory processing. Shorter EP latencies to stimuli at the cued location might be an index of this mechanism. Overall, a faster sensory signal would direct resource allocation, triggering sensory enhancement at the cued location (and, possibly, inhibiting competing neural circuits devoted to the analysis of

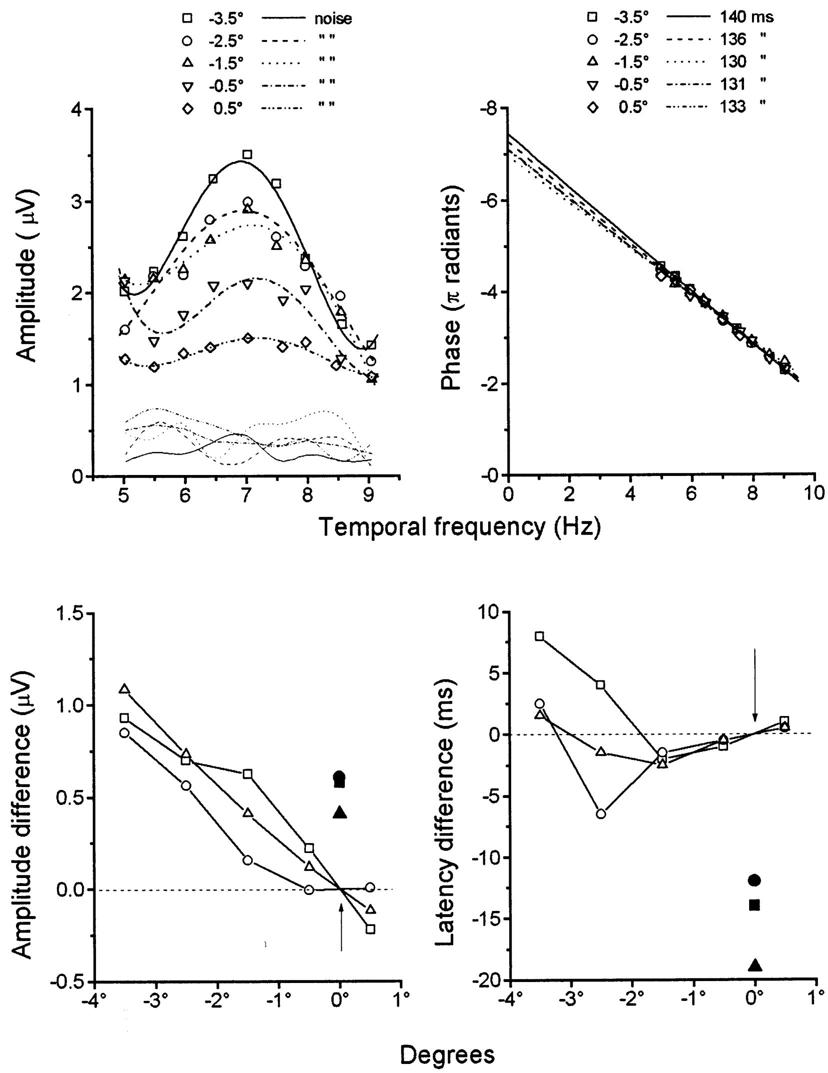

Fig. 5. Control experiment of eye movements with steady-state VEPs. The top of the figure shows the amplitude and latency data for one subject at the various fixation point positions. Negative degree values (in the upper labels) indicate displacements towards the left, where the grating was displayed. Note the systematic increment of amplitude (left part of the figure) and the small variation of latency (right part of the figure). Data from three subjects are reported with different symbols at the bottom. The positions of the fixation point are reported on the abscissa. The arrows indicate the location of the fixation point used in the previous experiment on attention. As above, negative values indicate that the fixation point was shifted towards the grating. At − 1.5°, the fixation point was on the edge of the grating. The VEPs amplitudes recorded at the nine temporal frequencies were averaged to obtain a mean value for each eccentricity and for each subject. The differences of the mean amplitude (left part of the figure) or the latency (right part of the figure) with respect to the reference values of each subject are reported on the ordinate. The reference values were the amplitude and the latency recorded when the fixation point was in the same position used in the previous experiment on attention, i.e. 0° on the abscissa. Positive values indicate increments with respect to the reference. Negative values indicate decrements. For comparison, filled symbols report the increase in amplitude and the shortening of the latency observed in the same subjects when attention was manipulated.

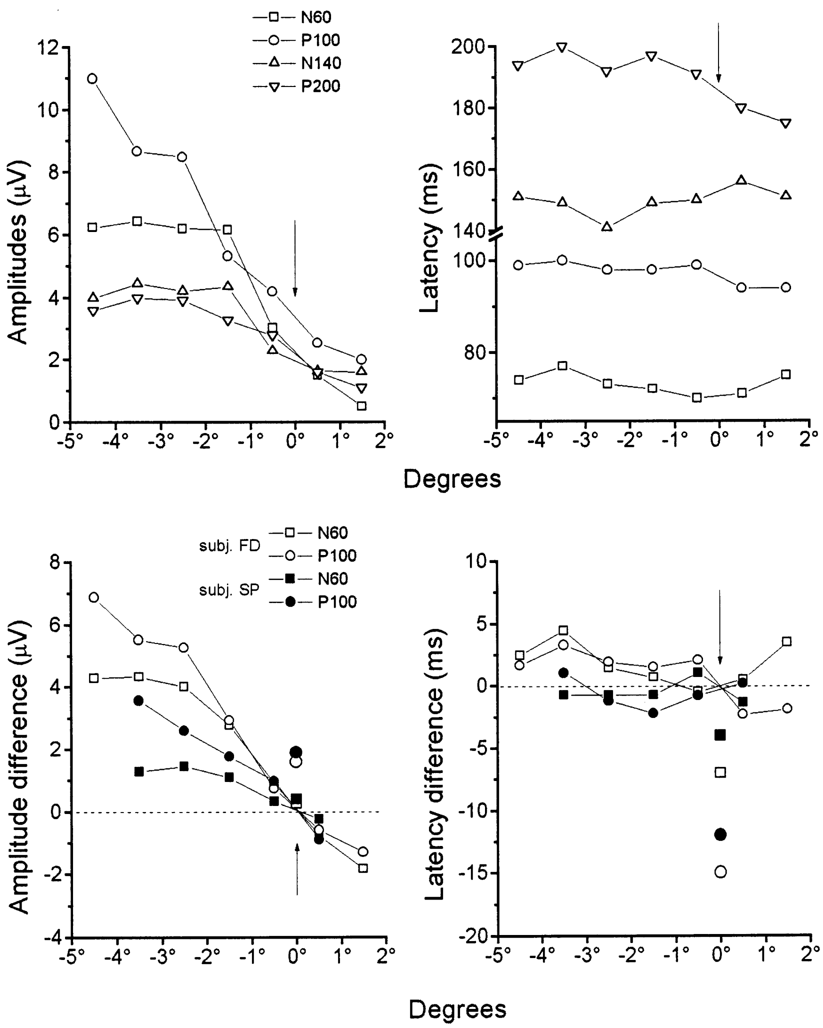

Fig. 6. Control experiment of eye movements with transient VEPs. Top of the figure: amplitude and latency data (recorded at Oz) for the various VEP components for one subject. Bottom: the amplitude and latency data of components N60 and P100 (averaged across O1, O2 and Oz) for two subjects (filled and open symbols) are reported. Abscissa and ordinate: as in Fig. 5. For comparison are reported the increase in amplitude and the shortening of the latency observed for the two components in the same subjects when attention was manipulated.

other portions of space). To this respect, it may be noted that the shortening of the VEP latency observed in the present work is similar in size to the temporal advantage by sustained attention measured in psychophysical studies (Hikosaka et al., 1993).

A possible objection to the view that latency is modulated by attention is that the changes in latency observed in the VEP components are caused by a change in the amplitude of other components. For instance, the shorter latency of N60 could be caused by a larger P100. This latter would cancel the later part of N60, thereby producing an apparent shift in peak latency of N60. It is difficult to reject this objection using the present technique (a more dense electrodes array and current density study would be necessary to identify the sources); however, there are cases in which such a prediction fails. For instance, when the fixation point is moved on the grating, both P100 and N60 grow but this latter much less (see Fig. 6, bottom left). However, in this case there is no shift of peak latency of N60 (see Fig. 6, bottom right). Thus, an interpretation in terms of spurious effect due to voltage subtraction cannot account for the general pattern of results.

Overall, the present results are in agreement with the idea that attentional effects are based on both enhancement and priority mechanisms. In particular, the research confirms a previous observation on amplitude increment and shows that speed of stimulus processing in the attended space is increased. It should be noted that these results are compatible with those expected on the basis of a gain mechanism model analogous to that described for contrast, where an increment of contrast produces an increment of amplitude and phase-advance (Shapley & Victor, 1978).

A further speculation might be proposed, based on the observation that the effect of attention on latency was present even in the component N60. Amplitude and latency effects were dissociated in this wave, with no modulation of attention on amplitude, as previously reported (e.g. Hillyard et al., 1995, pp. 674–675). This suggests that the effect of attention on the speed of transmission might act earlier in the visual system that the mechanism responsible for amplitude enhancement, perhaps triggering the latter.

The localisation in the brain of these effects of attention is still an open question. It is generally held that the enhancement of neural activity takes place at the level of the extra-striate cortex (Heinze et al., 1994). However, there is recent evidence, based on fMRI response, showing that spatial attention modulates activity in the primary visual cortex (Gandhi, Heeger & Boyton, 1998; Watanabe, Sasaki, Miyauchi, Putz, Fujimaki, Nielsen, Takino & Miyakawa 1998) and this view is supported also by a single cell study in monkey (Roelfsema, Lamme & Spekreijse, 1998). To our knowledge no data are currently available on the effect on latency. N60, the earliest wave modulated by attention, has been associated with activation of stellate cells by thalamic afferences in V1 (Schroeder, Tenke, Givre Arezzo & Vaughan, 1991); however, the possible contribution of other areas to the recorded VEP cannot be excluded, due to the existence of fast parallel afferences from subcortical to cortical structure (e.g. Givre, Schroeder & Arezzo, 1994; Ffytche, Guy & Zeki, 1995). Overall, while it is difficult to localise unequivocally the observed effects of attention in the brain, the present study suggests that they occur at an earlier stage than previously thought.

Previous studies have failed to detect the effect of attention on VEP latency, while amplitude variations have been generally observed. The control experiments permit excluding that our data are a spurious effect due to poor control of fixation. Indeed, for both transient and steady-state VEPs, the latency was roughly independent or only slightly modulated by moving the fixation position. Further, the shift of the fixation point had a large and more systematic impact on VEPs amplitude than on VEPs latency and enhanced all VEP components, while attention did not enhance N60. Thus, the well-known amplitude enhancement effect of attention is more prone to be spurious than the latency effect.

The failure to observe latency effects in previous studies might be due to their small size and to the different experimental conditions used. In the present study attention was tonically maintained at the same location and not shifted across locations. VEPs were recorded from a task-irrelevant, large, continuously displayed contrast-reversed grating of high contrast. Further, the contrast-reversal condition, differently from onset-offset presentation generally used in studies on attention, produces motion perception even at low temporal frequencies. The involvement of the motion system in the latency effect should be considered. This could be more pronounced at high temporal frequencies activating the fast-transmission magnocellular visual pathway. The presence of a larger attentional effect with steady-state than with transient stimulation might be due to a major involvement of the magnocellular pathway in the former case. Further, in brain damaged patients with attention deficits (neglect), specific damage to the magno pathway was detected (Spinelli, Angelelli, De Luca & Burr, 1996; Doricchi, Angelelli, De Luca & Spinelli, 1996). Thus, it might be proposed that priority order for the processing of sensory signals driven by spatial attention might rely on the fast-transmission magnocellular pathway.

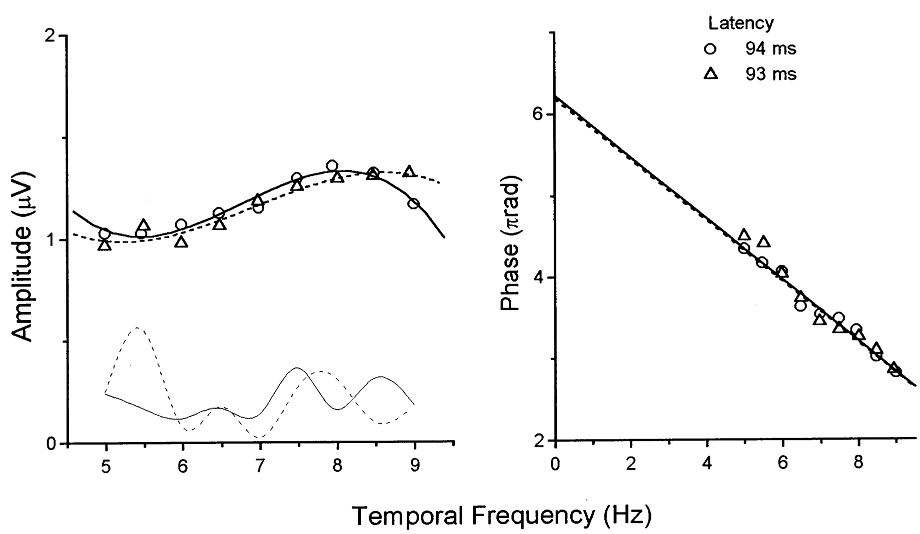

Fig. 7. Control experiment to measure the effect of the physical change of the stimulus due to the presence/absence of the target. The grating was presented in the LVF; the target was absent (open symbols) or it was superimposed on the grating (filled symbols). Amplitude and phase data are reported. On the left bottom the simultaneously recorded noise signals are reported.

Acknowledgements

Research supported by grants from C.N.R. and Ministero della Sanità. We are grateful to David Burr, Concetta Morrone, Gino Pizzamiglio and Pierluigi Zoccolotti for comments on an earlier version of the manuscript.

References

Bashinski, H. S., & Bacharach, V. R. (1980). Enhancement of perceptual sensitivity as the result of selective attending to spatial locations. *Perception and Psychophysics*, *28*, 241–248.

Campbel, F. W., & Maffei, L. (1970). Electrophysiological evidence for the existence of orientation and size detectors in the human visual system. *Journal of Physiology* (*London*), *192*, 345–358.

Doricchi, F., Angelelli, P., De Luca, M., & Spinelli, D. (1996). Neglect for low luminance contrast stimuli but not for high colour contrast stimuli: a behavioural and electrophysiological case study. *NeuroReport*, *7*, 1360–1364.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.

Ffytche, D. H., Guy, C. N., & Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. *Brain*, *118*, 1375–1394.

Gandhi, S. P., Heeger, D. J., & Boyton, G. M. (1998). Spatial attention in human primary visual cortex. *Investigative Ophthalmology and Vision Science* (*Supplement*), *39*, S1130.

Givre, S. J., Schroeder, C. E., & Arezzo, J. C. (1994). Contribution of extrastriate area V4 to the surface-recorded flash VEP in the awake macaque. *Vision Research*, *34*, 415–438.

Heinze, H. J., Mangun, G. R., Burchert, W., Hinrichs, H., Scholz, M., Munte, T. F., Gos, A., Scherg, M., Johannes, S., Huneshagen, H., Gazzaniga, M. S., & Hillyard, S. A. (1994). Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature*, *372*, 543–546.

Hikosaka, O., Miyauchi, S., & Shimojo, S. (1993). Focal visual attention produces illusory temporal order and motion sensation. *Vision Research*, *33*, 1219–1240.

Hillyard, S. A., Mangun, G. R., Woldorff, M. G., & Luck, S. J. (1995). Neural systems mediating selective attention. In M. S. Gazzaniga, *The cognitive neurosciences* (pp. 665–681). Cambridge, MA: Massachussetts Institute of Technology.

Luck, S. J., Fan, S., & Hillyard, S. A. (1993). Attention-related modulation of sensory-evoked brain activity in visual search task. *Journal of Cognitive Neuroscience*, *5*, 188–195.

Mangun, G. R., & Hillyard, S. A. (1990). Electrophysiological studies of visual selective attention in humans. In A. B. Scheibel, & A. F. Wechsler, *Neurobiology of higher cognitive function* (pp. 271–295). New York: Guildford.

Morgan, S. T., Hansen, J. C., & Hillyard, S. A. (1996). Selective attention to stimulus location modulates the steady-state visual potential. *Proceedings of the National Academy Science USA*, *93*, 4770–4774.

Morrone, M. C., Burr, D. C., & Fiorentini, A. (1993). Development of infant contrast sensitivity to chromatic stimuli. *Vision Research*, *33*, 2535–2552.

Morrone, M. C., Fiorentini, A., & Burr, D. C. (1996). Development of the temporal properties of visual evoked potentials to luminance and colour contrast in infant. *Vision Research*, *36*, 3141–3155.

Näätänen, R. (1990). The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function. *Behavioral and Brain Sciences*, *13*, 201–288.

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, *29*, 1631–1647.

Porciatti, V., Burr, C. D., Morrone, M. C., & Fiorentini, A. (1992). The effects of ageing on the pattern electroretinogram and visual evoked potential in humans. *Vision Research*, *32*, 1199–1209.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.

Posner, M. I. (1995). Attention in cognitive neuroscience: an overview. In M. S. Gazzaniga, *The cognitive neurosciences* (pp. 615–624). Cambridge, MA: Massachussetts Institute of Technology.

Regan, D. (1966). Some characteristics of average steady-state and transient responses evoked by modulated light. *EEG Clinical Neurophysiology*, *20*, 238–248.

Roelfsema, P. R., Lamme, V. A. F., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, *395*, 376–380.

Schroeder, C. E., Tenke, C. E., Givre, S. J., Arezzo, J. C., & Vaughan Jr, H. G. (1991). Striate cortical contribution to surface-recorded pattern-reversal VEP in alert monkey. *Vision Research*, *31*, 1143–1157.

Shapley, R. M., & Victor, J. D. (1978). The effect of contrast on the transfer properties of cat retinal ganglion cells. *Journal of Physiology* (*London*), *285*, 275–298.

Silberstein, R. B., Schier, M. A., Ciorciari, J., Pipingas, A., Wood, S. R., & Simpson, D. G. (1995). *Brain Topography*, *3*, 337–347.

Spekreijse, H., Estevez, O., & Reits, D. (1977). Visual evoked potentials and the physiological analysis of visual processes in man. In J. E. Desmedt, *Visual evoked potentials in man: new development* (pp. 16–89). Oxford: Clarendon Press.

Spinelli, D., Angelelli, P., De Luca, M., & Burr, D. C. (1996). VEPs in neglect patients have longer latencies for luminance but not for chromatic patterns. *NeuroReport*, *7*, 815–819.

Spinelli, D., Burr, D. C., & Morrone, M. C. (1994). Spatial neglect is associated with increased latencies of visual evoked potentials. *Visual Neuroscience*, *11*, 909–918.

Spinelli, D., & Di Russo, F. (1996). Visual evoked potentials are affected by trunk rotation in neglect patients. *NeuroReport*, *7*, 553–556.

Watanabe, T., Sasaki, Y., Miyauchi, S., Putz, B., Fujimaki, N., Nielsen, M., Takino, R., & Miyakawa, S. (1998). Attention-regulated activity in human primary cortex. *Journal of Neurophysiology*, *79*, 2218–2221.

Woldorff, M., Hansen, J. C., & Hillyard, S. A. (1987). Evidence for effects of selective attention to the midlatency range of the human auditory event related potential. *EEG Clinical Neurophysiology*, *40*, 146–154.

Woldorff, M., & Hillyard, S. A. (1991). Modulation of early auditory processing during selective listening to rapidly presented tones. *EEG Clinical Neurophysiology*, *79*, 170–191.