



Automatic gain control contrast mechanisms are modulated by attention in humans: evidence from visual evoked potentials

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Abstract

This study investigated the effect of attention on the contrast response curves of steady-state visual evoked potentials (VEPs) to counter-phased sinusoidal gratings. The 1 cyc/deg gratings were modulated either in luminance or chromaticity (equiluminant red-green). The luminance grating counter-phased at 9 Hz (to favour activation of the magno-cellular system), and the chromatic grating at 2.5 Hz (to favour activation of the parvo-cellular system). Attention was directed towards the gratings (displayed in the left visual field) by requiring subjects to detect and respond to randomly occurring changes in contrast. In the control condition, attention towards the grating was minimised by requiring subjects to detect a target letter amongst distracters briefly flashed in the contra-lateral visual field. Attention increased VEP amplitudes for both luminance and chromatic stimuli, more so at high than at low contrasts, increasing the slope of the contrast amplitude curves (over the non-saturating range of contrasts). The estimates of contrast threshold from extrapolation of amplitudes were unaffected by attention. Attention also changed the VEP phases, but only for luminance gratings, where it acted to reduce the magnitude of phase advance with contrast. Attention had no effect on the average phases for chromatic gratings. The results are consistent with the notion that attention acts on cortical gain control mechanisms, which are known to be different for the magno- and parvo-cellular systems. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

When we attend to an object, even without moving our eyes (covert attention), the processing of the object of interest becomes more efficient in many ways. Reaction times become shorter (Posner, 1980), and stimuli appear to occur earlier than non-attended events ('law of prior entry': Titchener, 1908; Hikosaka, Miyauchi, & Shimojo, 1993), and discrimination can also improve (e.g. Bashinski & Bacharach, 1980; Shaw, 1984; Muller & Findlay, 1987; Downing, 1988; Nakayama & Mackeben, 1989; He, Cavanagh, & Intrilligator, 1996; Lee, Koch, & Braun, 1997; Yeshurun & Carrasco, 1998). For an extensive up-to-date review of the effects of attention on perceptual processes, the reader is referred to Pashler (1998).

Several lines of research have led to the suggestion that attention acts as a sensory gain control mechanism, modulating the flow of information differentially between attended and unattended regions. Psychophysical studies (Lu & Doshier, 1998; Lee, Itti, & Braun, 1999) have shown that contrast thresholds in the presence of mask or noise can be improved by attention, implying a change in contrast gain control. However, other studies show that absolute contrast threshold cannot be enhanced by attention and that contrast gain modulation is not necessarily implicated to explain the attentional improvement at supra-threshold contrast (Foley & Schwarz, 1998). Neurophysiological studies on monkey (Treue & Martinez, 1998; Treue & Maunsell, 1999; McAdams & Maunsell, 1999) also show an increase of the neuronal response both for area V4 and MT. For MT cells, the tuning to direction during attention change in a multiplicative manner, as pre-

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dicted by a gain modulation. However, very little is known about the characteristics of the modulating mechanism. Imaging studies also showed attention-related increase of activation in multiple visual areas including primary visual cortex (Corbetta, Miezin, Shulman, & Petersen, 1991; Watanabe et al., 1997, 1998; Tootell, et al., 1998; Boynton, Demb, Glover, & Heeger, 1999; Gandhi, Heeger, & Boynton, 1999; Martinez, et al., 1999; Sengpiel & Hubener, 1999; Somers, Dale, Seiffert, & Tootell, 1999).

Strong support for the notion of attention modulating the gain of sensory processes comes from evoked potential studies, both auditory and visual. Attention enhances the amplitude of visual and auditory potentials (for a review, see Hillyard, Mangun, Woldorff, & Luck, 1995), and decreases their latency (Di Russo & Spinelli, 1999a). Attention also affects steady-state VEPs to counter-phased sinusoidal gratings over a wide range of temporal frequencies, increasing amplitude and decreasing phase consistent with an acceleration of the response by about 10 ms (Di Russo & Spinelli, 1999a). The decrease in response latency was observed only for grating modulated in luminance, not in chromatic contrast (Di Russo & Spinelli, 1999b). That attention modulates response latency is also supported by data in patients with an attentional for contra-lesional space deficit (hemineglect) consequent to brain lesions. The VEPs to stimuli located in the contra-lesional, neglected hemifield have latencies longer than those to ipsilesional, non-neglected stimuli (Spinelli, Burr, & Morrone, 1994; Angelelli, De Luca, & Spinelli, 1996); this delay was present only for luminance modulated stimuli, not for chromatic modulated stimuli (Spinelli, Angelelli, De Luca, & Burr, 1996).

The effect of attention on VEP amplitude and latency suggests that attention may play a role in regulating gain control mechanisms operating in human cortex. Automatic gain control mechanisms for contrast are present at several levels in the visual system, from the retina to the visual cortex (Shapley & Victor, 1978, 1979, 1981; Victor & Shapley, 1979; Sclar, 1987; Bernardete, Kaplan, & Knight 1992; Reid, Victor, & Shapley, 1992). This control, specific for M-, but not for P-pathways, is mediated by feedback loops that cause the non-linear increment of the response amplitude and phase advance with increasing luminance contrast (Shapley & Victor, 1981; Bernardete & Kaplan, 1999; Bernardete et al., 1992; Lee, Pokorny, Smith, & Kremers, 1994). No data are available for chromatic modulated stimuli at cortical level.

Automatic gain control mechanisms have been proposed to explain a variety of phenomena, such as saccadic suppression (Burr & Morrone, 1996) and cross-orientation inhibition and parallel-orientation

masking effects that require divisive inhibition (Morrone, Burr, & Maffei, 1982; Morrone & Burr, 1986; Burr & Morrone, 1987; Morrone, Burr, & Speed, 1987; Bonds, 1989; Carandini & Heeger, 1994; Carandini, Heeger, & Movshon, 1997). Making use of mechanisms already in place for other functions may be a very elegant and economic solution to achieve different goals, from saccadic suppression to enhancement by attention (Lee et al., 1999).

The purpose of this study was to use VEPs to examine how attention may affect the cortical mechanisms that control contrast gain. We used both luminance and colour stimuli, suitably modulated at high and low temporal frequencies, to privilege the activation of magno- and parvo-cellular pathways, to investigate possible differences in their control of contrast gain (Derrington & Lennie, 1984; Merigan, 1989; Lee, Pokorny, Smith, & Valberg, 1990).

2. Material and methods

2.1. Stimuli

VEPs were recorded to counter-phased sinusoidal gratings, displayed to the left visual field. Attention was directed towards the gratings by requiring subjects to detect and respond to randomly occurring changes in their contrast (about 20 changes on each run). In the control condition, attention was directed away from the gratings by requiring subjects to detect a target letter amongst distracters briefly flashed in the contralateral visual field.

The gratings were horizontal, 1 cyc/deg spatial frequency and subtended 9 deg × 9 deg of visual field, displayed continuously in the left visual field with its inner edge at an eccentricity of 3 deg. The grating contrast was modulated either in luminance (yellow–black) or in chromaticity (red–green). For the luminance condition, the temporal frequency was chosen separately for each subject to produce maximum VEP (always between 8 and 9.5 Hz). Michelson contrast varied between 1 and 32%. Red–green patterns were obtained by superimposing out-of-phase isochromatic red–black and green–black gratings of identical contrast. Yellow–black gratings were obtained by superimposing the same gratings in phase. For details of the chromatic stimulus generation, see Morrone, Burr, and Fiorentini (1993). The average luminance was 16 cd/m², and the C.I.E. co-ordinates at V_λ equiluminance were $x = 0.61$, $y = 0.35$ and $x = 0.28$, $y = 0.60$ for the red and green phosphors, respectively. For the colour condition, the temporal frequency was constant (2.5 Hz), and the contrast of each stimulus, calculated as the mean square root of L and M cone contrast, varied between 1% and 8% (Smith &

Pokorny, 1975). The ratio of the red luminance over the sum of the red and green luminance ($R/(R + G)$) was used to measure the subjective equiluminant point of the subjects, evaluated by standard flicker photometry. Equiluminant points varied between 0.46 and 0.56 for the various subjects. In addition, VEPs were recorded (at 8 Hz) for each subject at the corresponding flicker-photometry equiluminant point and at two other nearby points, to select the red–green ratio that generated the minor VEP amplitude (objective equiluminant value; see Morrone et al., 1993; Fiorentini, Burr, & Morrone, 1991). Individual VEP amplitudes as a function of red–green ratio are summarized in Fig. 1. There was a close correspondence between subjective and objective equiluminant point evaluation.

2.2. Procedure

Subjects fixated a central spot, and without moving their eyes performed one of the following two tasks. In the attended condition, they were required to detect and signal increments and decrements of the contrast of the counter-phased grating (pressing with the right and left thumbs one of two keys) presented in the left visual field (inner edge 3 deg), ignoring the display to the

right. In the unattended condition, they were required to signal the presence of the letter O within a 3×3 array of distracters (letter F), flashed in the right visual field. Each letter subtended 0.25 deg within an array of 1.2 deg presented for 100–200 ms at random intervals (about 36 presentations in 60 s).

A short training period familiarized subjects with the task while keeping fixation. Eye movements were monitored through a camera, with a zoom lens magnifying one eye of the subjects. Correct fixation was calibrated at the beginning of the each trial. The experimenter recorded the number of gaze shifts occurring in each run and gave feedback to the subject during the experiment.

VEPs were recorded during attended and unattended conditions, alternated in successive runs, with a short break in between. Each run lasted 60–90 s, with about 20 changes of contrast. VEPs to stimuli of various contrast levels were averaged in different files (over 20–60 sums), discarding the period immediately preceding and following the contrast change. Several runs were made for each condition in order to average responses to at least 180 stimulus repetitions at medium to high contrasts and 600 stimulus repetitions at low contrast.

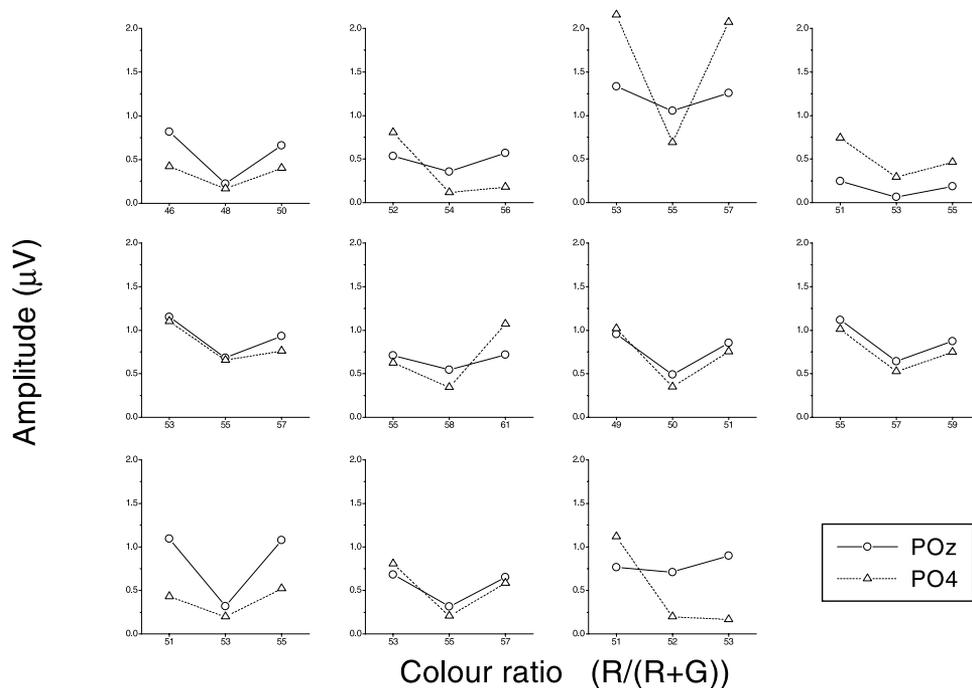


Fig. 1. Measurement of equiluminant point by VEP recording. VEP amplitudes as a function of the ratio of the red luminance over the sum of the red and green luminance ($R/(R + G)$). Data were recorded at two electrodes (POz and PO4, reported by circles and triangles, respectively) in 11 subjects during a preliminary experiment devised to measure equiluminant point (see Section 2). For each subject, the central point corresponds to the flicker photometry isoluminant setting. Temporal frequency: 8 Hz; rms contrast 5% at equiluminance. The colour ratio producing the lowest amplitude potential was taken as the equiluminant point and was used in the following experiment with attention and chromatic modulated gratings.

2.3. Subjects

Two different groups of subjects participated in the experiment. Eleven subjects (mean age 26.2; seven females) were recorded in the luminance-contrast condition and eleven subjects (mean age 25.4; eight females) in the chromatic-contrast condition. All subjects had normal or correct-to-normal vision.

2.4. Task accuracy

Contrast changes were detected on average in 81% of the trials (range 75%–90%); letter discrimination was successfully on average in 76% of the trials (range 69%–89%). The median of the number of gaze shift was 1 per run (range 0–5) in the attended condition and 2 per run (range 0–7) in the unattended condition. The median of the number of blinks was 2 per run (range 0–6) in the attended condition and 1 per run (range 0–6) in the unattended condition.

2.5. VEP recording and data analysis

Steady-state VEPs were recorded from two active scalp electrodes, one on the midline (POz) and one on the right side (PO4), with FCz reference and CPz ground (10–10 system). Signals were amplified (50,000 fold), band-pass filtered (1–30 Hz) and digitised at 64 samples/period. Responses were averaged in packets of 20 sums (for luminance) and 10 sums (for chromatic stimuli). Nine to 30 packets were averaged to obtain the final VEP. The steady-state VEP waveform is roughly sinusoidal and is well described by the amplitude and phase of the second harmonic component (Campbell & Maffei, 1970). The computer performed an on-line Fourier analysis to calculate the amplitude and the phase of the second harmonic. Standard deviation of amplitude and phase were calculated based on the scatter of the various packets contributing to the final VEP. The computer averaged also 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, to assess VEP reliability during the experiment. If the signal-to-noise ratio was very low, an additional recording was performed. The signal-to-noise ratio was calculated for each packet of 20 sums (for luminance) or 10 sums (for colour). Packets with a low signal-to-noise ratio were eliminated off-line (see Morrone et al., 1993 for details).

2.6. Control experiment

As the letters in the visual search task were desynchronized with respect to the grating reversal, they should not contribute to the VEP recording. However, to be certain that they had no effect, we measured the

contribution of the letters to the recorded VEP, measured in synchrony with the grating contrast reversal (9 Hz), but with the grating contrast set to zero. As expected, the VEP amplitude in this condition was at the level of noise at both electrodes for all three tested subjects.

3. Results

3.1. Luminance contrast: VEP amplitude

Fig. 2 reports the amplitudes and phases of one subject recorded in the attended and unattended conditions as a function of contrast for the two electrode positions. When the subject attended to the changes in grating contrast, the VEP amplitudes were generally higher than those recorded from the same stimulus with the subject attending to the stimulus in the opposite visual field. The increase is particularly evident at high saturating contrasts, and is stronger for the electrode contralateral (PO4) to the recording stimulus. The majority of subjects showed a similar effect. Fig. 3 (top) shows the data averaged across subjects and shows an increase in the amplitude of the response at all contrasts by attention. However, the increment is stronger at higher contrasts.

In the contrast range below saturation, the amplitude can be well fitted by a linear regression (thick lines). The slopes of the contrast response curves in Fig. 3 (between 1% and 16% contrast) were steeper in the attended than in the unattended condition for both electrodes (0.66 vs. 0.49 at POz and 0.88 vs. 0.62 at PO4), indicating that attention modulates the gain of the response.

Not all subjects showed the same magnitude of effect. To quantify the variability, individual data were fitted in the non-saturated range of each subject by linear regression. This range varied considerably across subject and electrodes (in two cases being as low as 6%), but the same range was used for the attended and unattended conditions. The ratio between the slopes of the regression for the attended versus unattended condition expresses the gain amplification induced by attention. The mean ratios across subjects are 1.15 (± 0.08) at POz and 1.46 (± 0.1) at PO4. These values are similar to those obtained in the averaged amplitude data, indicating that the individual variability in the saturation range does not bias the slope estimate of the averaged amplitude data.

Fig. 4a shows the frequency distribution of ratios of the regression slopes for all subjects, pooled over electrodes. The distribution is skewed towards values greater than 1, with a mode at 1.4, mean of 1.31 and standard deviation of 0.32, indicating a steeper slope value in the attention condition. However, some sub-

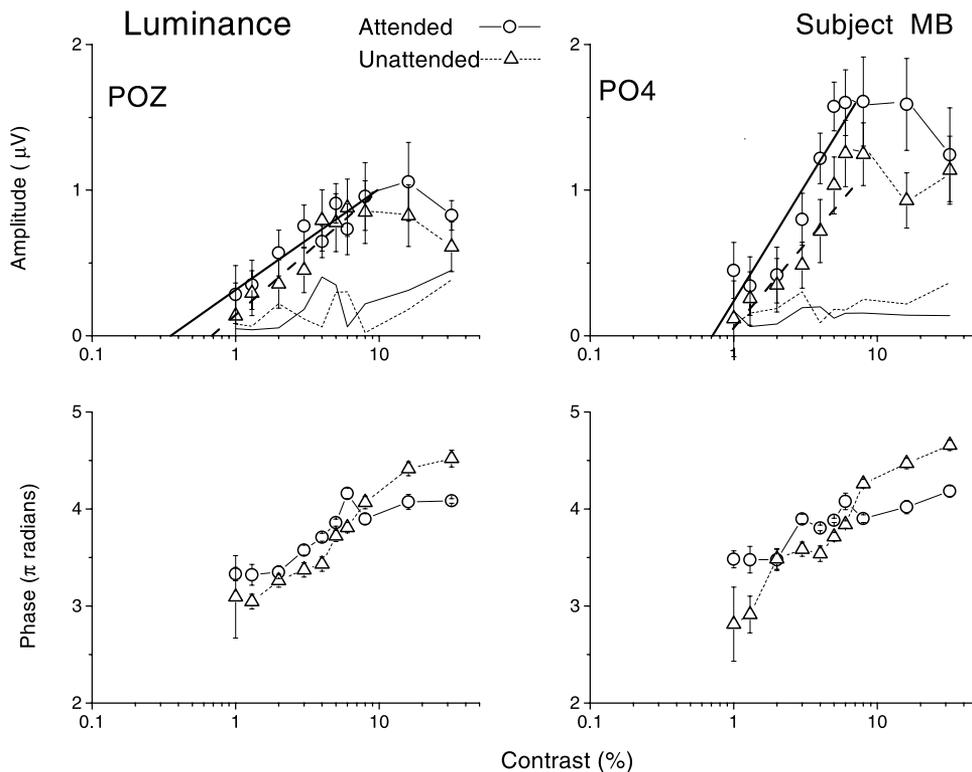


Fig. 2. Effect of attention on contrast–response curve for luminance grating (subject MB). Top: VEP amplitudes and standard deviation as a function of luminance contrast recorded at two electrode sites (POz and PO4, left and right part of the figure, respectively) in the two experimental conditions: attended (circles) and unattended (triangles). The noise level recorded in the two conditions is reported by continuous (attended) and dashed (unattended) lines. The contrast was reversed at 9 Hz. Linear fit in the non-saturated range (1%–8% at POz; 1%–6% at PO4), shown by the thick lines, was calculated by weighting each data point with the signal to noise reliability ratio (see Section 2). The slopes of the regression lines were 0.69 (attended) vs. 0.86 (unattended) at POz; 1.6 (attended) vs. 1.16 (unattended) at PO4. Correlation coefficients of the fit were 0.90 (attended) vs. 0.96 (unattended), 0.88 (attended) vs. 0.93 (unattended) for POz and PO4, respectively. Contrast thresholds estimated by extrapolation of the regression lines were: 0.35% (attended), 0.69% (unattended) at POz; 0.71% (attended), 0.90% (unattended) at PO4. Bottom: VEP phases and standard deviation in π radians as a function of luminance contrast. The phase advance with contrast at POz was 2π in the unattended condition and 1π in the attended condition; at PO4, it was 1.8π in the unattended condition and 0.7π in the attended condition. The slopes of the regression lines (not shown for clarity) in the range 1%–32% were 0.46 (attended), 1.18 (unattended), 0.41 (attended), 1.19 (unattended) at POz and PO4, respectively. Regression coefficients: 0.87, 0.98, 0.87, 0.95.

jects had no effect of attention and few subjects even opposite effects. For example, the subject data reported in Fig. 2 had a ratio lower than 1 (0.8) at the electrode POz.

The variability in the attention effect between subjects can also be evaluated statistically. An ANOVA performed on the raw amplitude data for all contrasts shows that VEPs amplitudes were larger ($F_{(1,10)} = 44.07$; $P < 0.0001$) in the attended condition with respect to the unattended condition (on average, 0.79 vs. 0.61 μV). Also, VEP amplitudes increased significantly with contrast ($F_{(9,90)} = 37.68$; $P < 0.0001$). However the interaction between the attention and the contrast factors was not significant, probably reflecting the fact that not all subjects showed a change of slope between the two conditions.

The intercept of the abscissa of the linear regression of VEP amplitude versus log contrast predicts the contrast threshold for detection (Campbell & Maffei, 1970). In the averaged data (Fig. 3), the intercepts of

the abscissa were close in the attended and unattended conditions, being 0.24% vs. 0.23% (at POz) and 0.54% vs. 0.46% (at PO4).

Intercept values were also calculated from the individual linear regressions. The mean of the estimates of contrast thresholds across subjects was 0.24 (± 0.05)% for the attended condition and 0.32 (± 0.08)% for the unattended condition at POz; 0.53 (± 0.06)% in the attended condition and 0.46 (± 0.07)% in the unattended condition at PO4. As for the slope estimates, the threshold estimates are very similar to those obtained by regression of the average amplitude data of Fig. 3. The frequency distribution of individual difference of threshold estimate is reported in Fig. 4b. The distribution is centred on 0% (S.D. = 0.17%), indicating no mean effect of attention on contrast threshold. Given an average threshold for the unattended condition of about 0.35%, the threshold changes in the standard deviation range by a factor of two.

Overall, both the individual and the average data suggest that attention induces a small but consistent increase in gain of the amplitude-contrast response curves, with no accompanying change in contrast threshold.

3.2. Phases

The lower panels of Figs. 2 and 3 show the phase response as a function of contrast. In both conditions, phase advances with increasing contrast, as previously observed (Burr & Morrone, 1987). For subject MB (Fig. 2), the phase advance is about 2π radians in the unattended condition, implying a response at highest contrast faster by about 56 ms (at 9 Hz) than at low contrast. In the attended condition, the phase advance with contrast was reduced to about 1π radians, corresponding to about 27 ms for this range of contrast. The two curves intercept at intermediate contrast values, with attention increasing phases at low contrast while decreasing them at high contrast. The data averaged across subjects (Fig. 3 bottom) show a similar trend.

An estimate of the overall phase advance can be obtained by fitting the data in Fig. 3 with a linear

equation. The fit was good for the averaged data, with coefficient R always above 0.90 for all conditions and electrodes. The slopes of the curves were 1.09 (attended) and 1.42 (unattended) π radians/log-unit of contrast at POz; 1.13 (attended) and 1.51 (unattended) π radians/log-unit of contrast at PO4. The reduction of phase advance due to attention was 0.33 π radians/log-unit of contrast at POz (corresponding to a latency change of 9 ms/log-unit contrast) and 0.38 π radians/log-unit of contrast at PO4 (corresponding to a latency change of 10.5 ms/log-unit contrast). Values obtained by fitting data over the range 1%–8% of contrast, where the phase changes more rapidly, gave a very similar result.

Given the variability between subjects, not all individual data could be reliably fitted by linear regression. However, the differences between the phase response at each contrast tended to vary linearly with contrast, and these were reliably fitted by linear regression, with the slope of the regression giving an index of phase change by attention. Fig. 4c shows the frequency distribution of the slopes pooled across electrodes. The distribution is skewed towards negative values with a mean of -0.34 (S.D. = 0.25) π radians/log-unit of contrast, in-

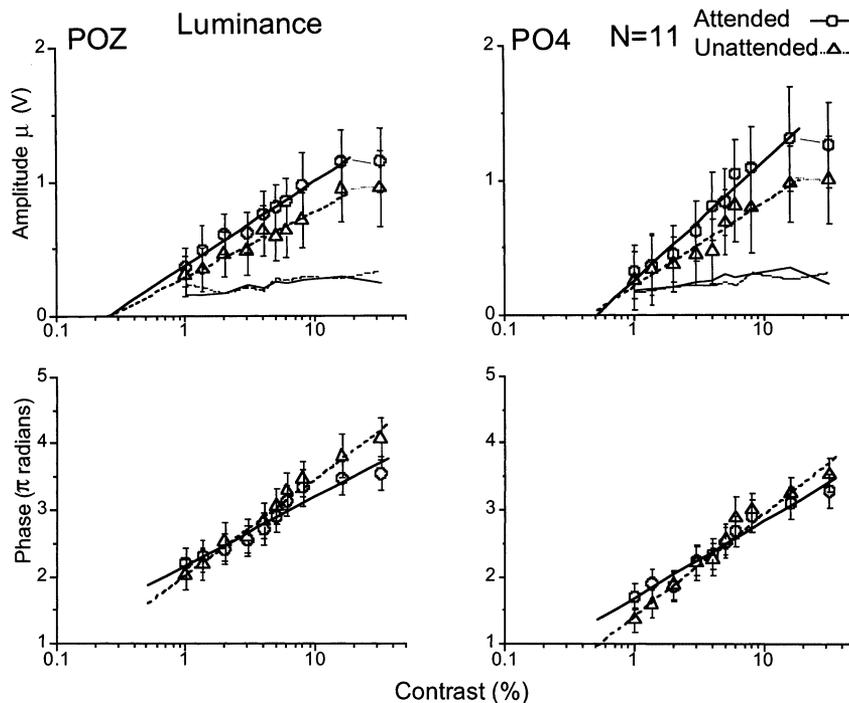


Fig. 3. Effect of attention on contrast–response curve for luminance gratings. Averaged data. Top: averaged ($n = 11$) VEP amplitudes and standard deviation as a function of luminance contrast. Symbols and figure details are the same as in Fig. 2. Linear fit in the non-saturated range (1%–16% at both electrodes) produced the following correlation coefficients: 0.99 (attended) and 0.98 (unattended) for POz; 0.98 (attended) and 0.96 (unattended) for PO4. Slopes of the regression lines were 0.66 (attended) and 0.49 (unattended) at POz; 0.88 (attended) and 0.62 (unattended) at PO4. Regression lines intercept the abscissa at 0.24% (attended) vs. 0.23% (unattended) at POz; 0.54% (attended) vs. 0.46% (unattended) at PO4. Bottom: averaged VEP phases and standard deviation in π radians as a function of luminance contrast. Regression coefficients of the linear fit of the data in the range 1%–32% were 0.93, 0.98, 0.96, 0.97. The slopes of the curves were 1.09 (attended) and 1.42 (unattended) π radians/log-unit of contrast at POz; 1.13 (attended) and 1.51 (unattended) π radians/log-unit of contrast at PO4. The phases advance with contrast, and attention reduces such advance.

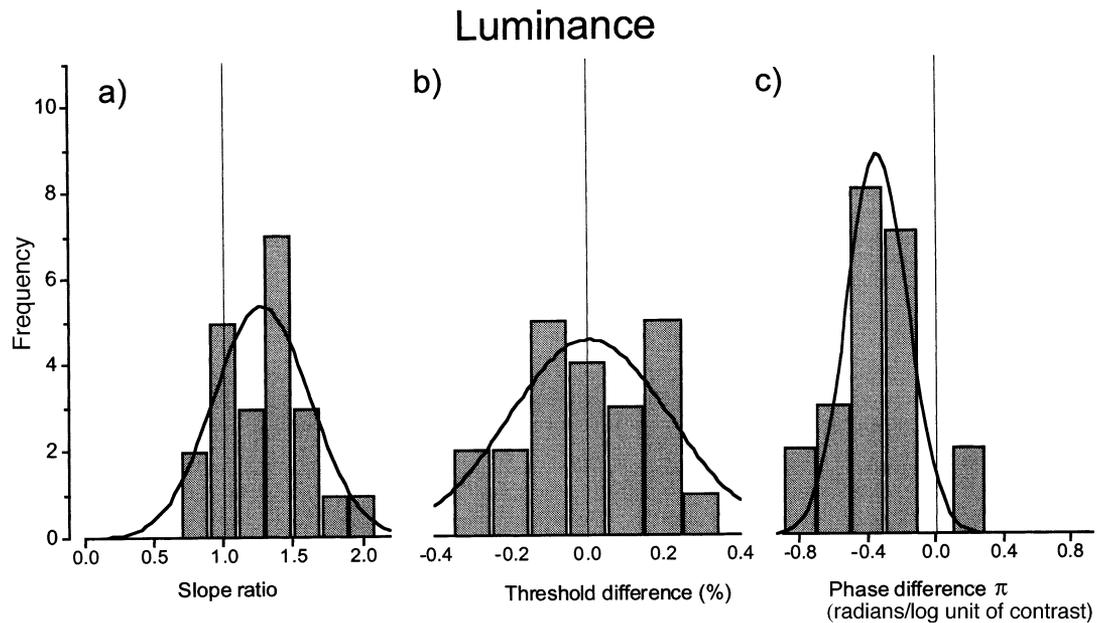


Fig. 4. Frequency distribution for data collected with luminance gratings. (A) Frequency distribution of individual ratios between the slopes of the regression for the attended versus unattended condition. The ratio expresses the gain amplification operated by attention. Data for 11 subjects, pooled over electrodes ($n = 22$). The peak of the distribution (1.4) is shifted towards positive values. The mean of the distribution is 1.31 (S.D. = 0.32). Note that in some cases, there is no effect of attention (ratio = 1), and two cases show the opposite effect (ratio = 0.8). (B) Frequency distribution of the individual threshold difference between attended and unattended condition pooled over electrodes. Thresholds were estimated by intercept values calculated from the individual linear regression fitting. The distribution is centred on 0% (S.D. = 0.17%), indicating no mean effect of attention on contrast threshold. (C) Distribution of the slopes of the regression of the individual phase differences pooled over electrodes. The mean of the distribution is -0.34 (S.D. = 0.25) π radians/log-unit of contrast, indicating a reduction of phase advance by attention. Only two cases showed null or positive slope. The straight lines indicate the point of no modulation by attention.

indicating a reduction of phase advance in the attended condition. Only two cases run counter this trend, showing a null or positive change of slope.

The individual phase data were also analysed statistically by ANOVA. The effect of contrast on the VEP phase was significant ($F_{(9,90)} = 108.51$; $P < 0.0001$). Attention was not significant as a main factor. However, the interaction between attention and contrast was significant ($F_{(9,90)} = 8.72$; $P < 0.0001$). Duncan's post-hoc test showed that attention changed the phase at low contrast (at 1% and 1.3%) and at high contrast (at 6%, 16% and 32%) in opposite directions.

Both the statistical and the analytic analysis confirm that attention systematically changes the phase of the response to luminance contrast, decreasing the phase advance and reducing the dependence of the processing time from contrast by about 10 ms per log-unit of contrast.

3.3. Chromatic contrast: amplitudes

Analyses similar to those described above were performed for the chromatic contrast modulated stimuli. The upper panel of Fig. 5 shows the VEP amplitudes of one subject recorded for the attended and unattended

conditions, and Fig. 6 shows the data averaged across 11 subjects.

For the chromatic stimuli, only the lower range of contrasts was tested for two reasons: as the low temporal frequency led to inherently long recording sessions, we focused mainly on the acquisition of low contrast data, more useful for evaluating both contrast thresholds and response curve gain; moreover, the equiluminance point can vary at a high contrast, due to an imperfect gamma correction of the display.

The amplitude response of Figs. 5 and 6 shows an enhancement with attention, similar to that observed with luminance contrast. The fitting of the averaged points was performed over the contrast range of 1%–4%, within which responses were not saturated at either electrode. The slopes of the contrast response curves were steeper in the attended condition than in the unattended condition: 1.15 vs. 0.98 (at POz) and 1.77 vs. 1.26 (at PO4). However, the overall distribution of the ratio of the slopes of the individual regression lines for attended versus unattended data in the non-saturating range (Fig. 7a) is bimodal with a peak at 1 and another at 1.6, with a mean at 1.5 (S.D. = 0.47). As for the luminance, the main effect of attention is to increase the slope of the amplitude response curve.

ANOVA on the amplitude data of all contrasts indicated VEPs amplitudes larger ($F_{(1,9)} = 55.49$; $P < 0.0001$) in the attended condition with respect to the unattended condition (on average, 1.17 vs. 0.95 μV). VEPs amplitudes increased with contrast ($F_{(7,70)} = 38.88$; $P < 0.0001$). The interaction between attention and contrast was significant ($F_{(7,70)} = 2.5$; $P < 0.05$), indicating that the effect of attention was not present at the lowest contrast (1%–2%) but was significant at higher contrasts, reinforcing the result obtained by linear fit of the response curve.

The intercepts of the abscissa calculated by linear regression of the averaged data (Fig. 6 top) were similar in the attended and unattended conditions, being 0.29% vs. 0.25% (at POz) and 0.56% vs. 0.44% (at PO4), respectively. This result was confirmed by the individual subject thresholds data, that were equal to $0.37\% \pm 0.05\%$ vs. $0.31\% \pm 0.04\%$ (at POz) and $0.58\% \pm 0.05\%$ and $0.44\% \pm 0.06\%$ (at PO4). Fig. 7b shows the distribution of the difference in threshold estimates, pooled across electrodes. The distribution, as for the luminance data, is centred on zero, showing no consistent effects of attention on threshold.

3.4. Phases

As for luminance, chromatic modulated gratings produce the phase response curve that advances with contrast by a substantial value, about 0.8π radians/log-unit of contrast corresponding to a delay of about 80 ms (for stimulus temporal frequency of 2.5 Hz). However, although the phase advance was substantial, it was not altered by attention. Fig. 7c shows the phase response averaged over all subjects. The points are all clearly in overlap, with a very slight uniform shift, but no change in slope. The linear regression in the attended condition, at the POz electrode, showed a phase advance of 0.79π radians/log-unit contrast, compared with 0.86π radians/log-unit in the unattended condition. At the PO4 electrode, the phase advance was 0.81π radians/log-unit contrast in the attended condition and 0.80π radians/log-unit in the unattended condition. Thus, the phase advance with contrast in the unattended condition was slightly larger (0.07π radians/log-unit) at POz and slightly smaller (-0.01π radians/log-unit) at PO4.

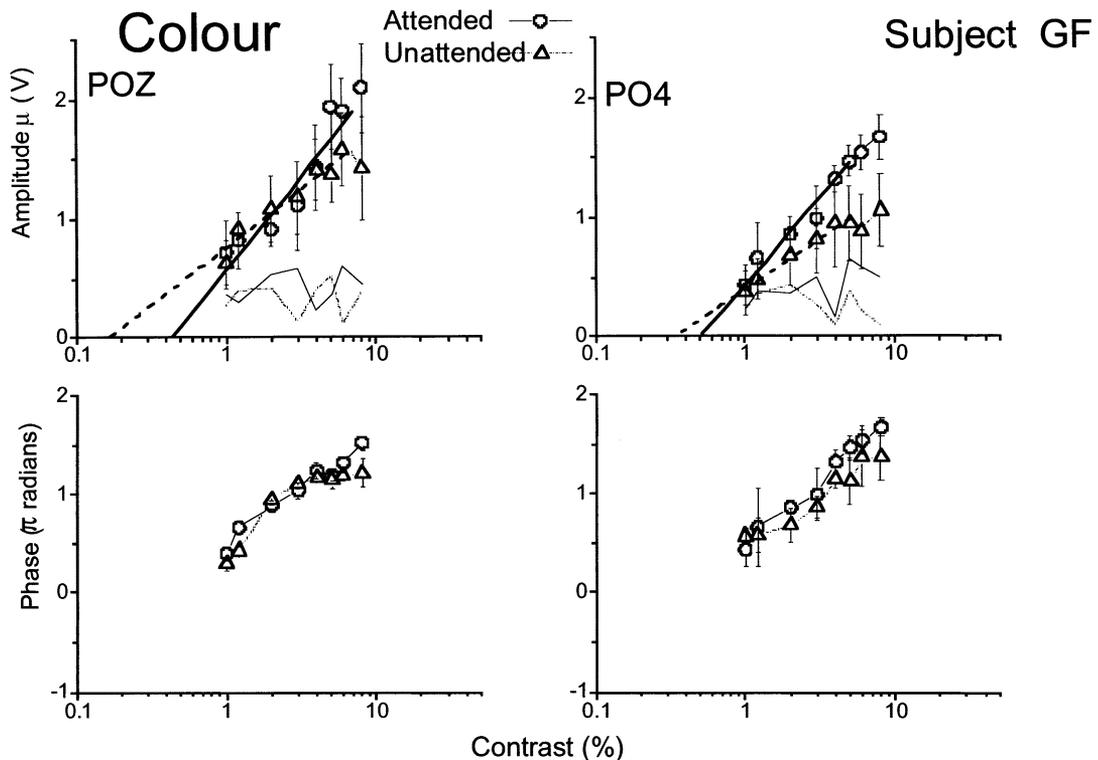


Fig. 5. Effect of attention on contrast–response curve for chromatic gratings (subject GF). Top: VEP amplitudes and standard deviation as a function of chromatic contrast recorded at two electrode sites in attended and unattended conditions. Symbols and details of the figure are the same as in Fig. 2. The contrast was reversed at 2.5 Hz. The linear fit in the non-saturated range (1%–6% at POz; 1%–5% at PO4) had the following correlation coefficients: 0.93 (attended) vs. 0.94 (unattended), 0.99 (attended) vs. 0.99 (unattended) for POz and PO4, respectively. The slopes of the regression lines were 1.56 (attended) vs. 1.08 (unattended) at POz; 1.46 (attended) vs. 0.92 (unattended) at PO4. Regression lines intercept the abscissa at 0.43% (attended) vs. 0.20% (unattended) at POz; 0.51% (attended) vs. 0.38% (unattended) at PO4. Bottom: VEP phases and standard deviation in π radians as a function of luminance contrast. The phase advance with contrast is not reduced by attention. The slopes of the regression lines (not shown) obtained by the linear fit were 1.02 (attended), 1.16 (unattended) at POz; 1.39 (attended) 0.91 (unattended) at PO4. Correlation coefficients: 0.98, 0.95, 0.99, 0.97.

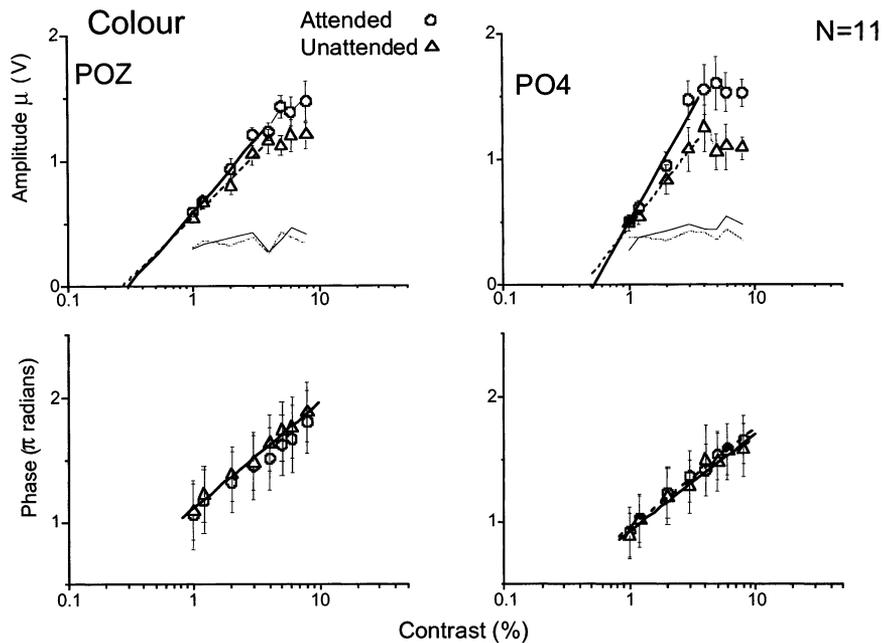


Fig. 6. Effect of attention on a contrast–response curve for chromatic gratings. Averaged data. Top: averaged ($n = 11$) VEP amplitudes and standard deviation as a function of chromatic contrast. A linear fit in the non-saturated range (1%–4% at both electrodes) produced the following correlation coefficients: 0.99 (attended and unattended) for POz; 0.98 (attended) and 0.96 (unattended) for PO4. The slopes of the regression lines were 1.15 (attended) and 0.98 (unattended) at POz; 1.77 (attended) and 1.26 (unattended) at PO4. Regression lines intercept the abscissa at 0.29% (attended) and 0.25% (unattended) at POz; 0.56% (attended) and 0.44% (unattended) at PO4. Bottom: averaged VEP phases and standard deviation in π radians as a function of chromatic contrast. Regression coefficients of the linear fit of the data in the range 1%–8% were 0.99 (attended and unattended at POz), 0.94 (attended) and 0.97 (unattended) at PO4. The slopes of the curves were 0.79 (attended) and 0.86 (unattended) π rad/log-unit of contrast at POz; 0.81 (attended) and 0.80 (unattended) π rad/log-unit of contrast at PO4. The phase advance with contrast is not changed by attention.

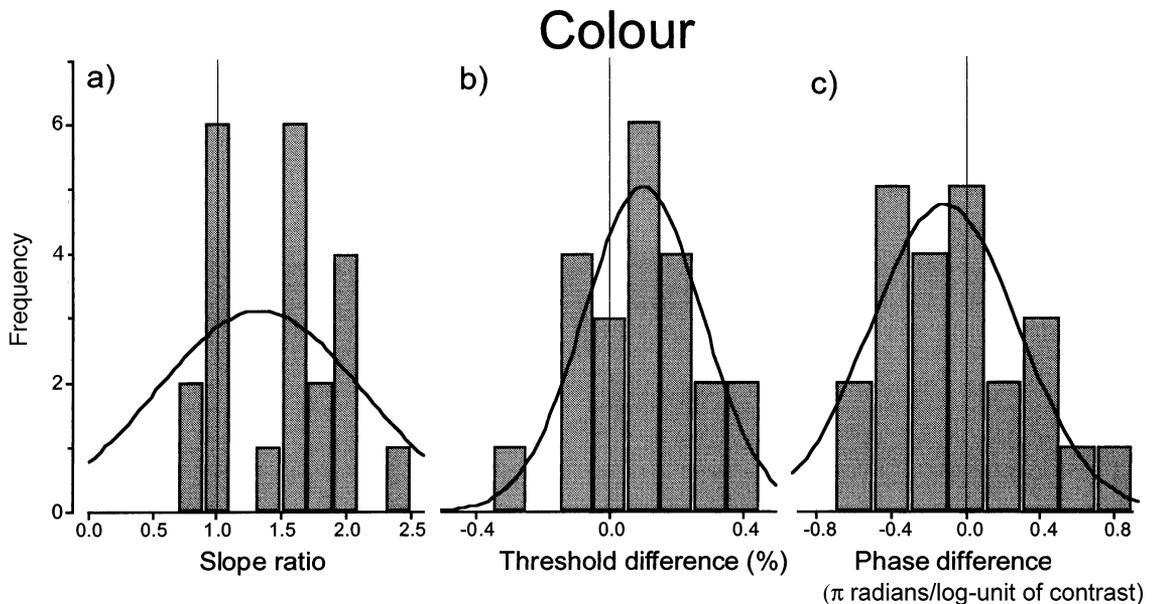


Fig. 7. Frequency distribution for data collected with chromatic gratings. (A) Frequency distribution of the individual ratios between the slopes of the regression (in the non-saturating range) for the attended versus unattended condition. Data for 11 subjects, pooled over electrodes ($n = 22$). The distribution is bimodal with a peak at 1 and another at 1.6; the mean of the distribution is 1.5 (S.D. = 0.47). The prevalent effect of attention is an increase in the response curve gain, but in some cases, no such increase is present. (B) Frequency distribution of individual threshold difference between attended and unattended condition pooled over electrodes. The distribution is centred on 0.1% (S.D. = 0.17%), indicating no mean effect of attention on contrast threshold. (C) Distribution of the slopes of the regression of the individual phase differences pooled over electrodes. The mean of the distribution is -0.02 (S.D. = 0.37 π radians/log-unit of contrast). The straight lines indicate the point of no modulation by attention.

Some subjects (such as the example of Fig. 5) do show a phase change with attention, usually uniform at all contrasts, but this was not in a systematic direction and averaged out in the pooled data. To be certain that attention produced no net change in slope of the phases of the contrast response curve, we plotted separately for each subject the difference in phase against contrast, and calculated this slope of this curve by linear regression (as for the luminance data). Fig. 7c shows the distribution of the slopes of the phase change for all 11 subjects. There is considerable scatter, but the distribution is clearly centred near zero (mean -0.02 , S.D. 0.37). An ANOVA showed a significant effect of contrast on VEP phases ($F_{(9,90)} = 118.87$; $P < 0.0001$), but attention was not significant as a main factor, nor was its interaction with contrast significant.

In summary, for the chromatic modulated stimuli, attention was effective in increasing the gain of the amplitude of the VEP response without systematically changing phase advance.

3.5. Noise level and standard deviation of VEP to luminance and chromatic contrast

One possibility is that the effects of attention on VEP amplitude result from an overall non-specific increase in the excitability of the neuronal circuitry. If this were so, it should result in an increase not only in the synchronous response, but also in the asynchronous response near the modulation frequency. To evaluate this hypothesis, we measured the increase in EEG amplitude at a frequency close to the response frequency (see Section 2), for the two conditions. The noise amplitude did not vary significantly with attention either for luminance or for colour. The values averaged over contrasts and subjects were: 0.23 vs. 0.23 μV at POz; 0.27 vs. 0.26 μV at PO4 for luminance stimuli and 0.37 vs. 0.34 μV at POz; 0.40 vs. 0.37 μV at PO4 for chromatic stimuli. Noise amplitude increased at higher luminance contrast ($F_{(9,90)} = 5.96$; $P < 0.0001$), while the increment was not significant for chromatic contrast.

We also evaluated the possibility that attention causes a higher response by reducing the response variability. As an index of response reliability, we took the estimated standard deviation of amplitude and phase values obtained by the scatter of subsets of the data (see Section 2).

ANOVA showed no effect of attention on the standard deviations of VEP amplitudes for both luminance and chromatic contrast. For luminance stimuli, the standard deviation was larger at the PO4 electrode than at POz (0.26 vs. 0.19 μV ; $F_{(1,10)} = 17.40$; $P < 0.005$). For chromatic stimuli, the standard deviations were larger at the PO4 electrode than at POz (0.45 vs. 0.33 μV ; $F_{(1,10)} = 16.42$; $P < 0.005$). Again, no effect of attention was present on standard deviation of phases for both

luminance and chromatic stimuli. For luminance stimuli, the variability of phases was larger at PO4 electrode (0.09 π radians) with respect to the POz electrode (0.14 π radians) ($F_{(1,10)} = 20.41$; $P < 0.005$). For chromatic stimuli, the variability of phases was larger at the PO4 electrode (0.33 π radians) with respect to the POz electrode (0.45 π radians) ($F_{(1,10)} = 16.42$; $P < 0.005$).

4. Discussion

Sustained spatial attention changed the VEP contrast response functions for both luminance and chromatic stimuli, but in different ways. In both cases, attending to the stimulus increased the amplitude of the VEPs multiplicatively, increasing the slope of the amplitude-response curves without affecting the extrapolated contrast threshold. However, only for luminance did attention reduce the phase advance of the contrast response curves. Apart from their theoretical interest, these results could be of practical importance in applying VEP techniques for clinical and infant work. There could well exist a modification of the VEP response, but this may reflect the variability in attention of the subject rather than an immaturity or pathology. In neglect patients, for example, the observed increase in VEP phases could reflect the inability of the subject to direct and engage attention in the neglected visual field (Spinelli et al., 1994; Angelelli et al., 1996; Spinelli et al., 1996).

Requiring subjects to monitor changes in contrast ensured that subjects attended to the stimulus that generated the response, rather than merely to the same spatial position of the stimulus. In the unattended condition, we engaged attention on a difficult search task away from the stimulus, as is often used in psychophysical attention paradigms. The clear effects of the VEP contrast response curves, particularly on phase responses, show that the tasks were effective in directing attention, and that attention affected primary visual function.

We controlled that the effect was not due to a gaze shift, by monitoring eye movements. We also showed that the amplitude increase did not cause an a-specific increase in EEG activity by measuring background EEG levels of similar frequencies. Nor did attention decrease the variability of the response, measured by the variance of amplitude and phase. These results point to a specific action of attention on gain mechanism, rather than damping the internal noise of the system.

We observed no change of contrast threshold estimated from the extrapolated VEP amplitudes. This agrees with several psychophysical studies showing very little change in absolute contrast thresholds (Foley & Schwarz, 1998; Carrasco, Pempeci-Talgar, & Eckstein, 2000). However, recent psychophysical studies show that increment contrast thresholds and thresholds measured in the presence of noise are affected by attention,

pointing to a change in the transducer function (Lu & Doshier, 1998; Lee et al., 1999). These authors propose that attention changes the shape of the contrast transducer function by modulating the contrast gain mechanism (although this idea has been challenged by Foley & Schwarz, 1998). Single cell recordings also point to attention modulating gain control mechanisms. Attention changes multiplicatively the orientation response curves of single cells of area V4 (McAdams & Maunsell, 1999) and contrast response of MT neurones (Treue & Martinez, 1998).

Two models have recently been proposed for the mediation of contrast gain control: one by Shapley and Victor (1981), the other by Carandini and Heeger (1994) and Carandini et al. (1997). In Shapley and Victor's model, contrast gain is automatically controlled by a feedback loop that changes the high-pass characteristics of the response. This model predicts an increase in response latency at low contrasts, as it changes the temporal constants of the feedback loop. In agreement with this prediction, many studies have shown that at various levels of the visual system, single cell response latency increases with stimulus contrast. The neuronal integration constant can change by 30–50 ms over the contrast range used in the present experiment (Shapley & Victor, 1981; Bernardete & Kaplan, 1999). The model of Carandini and Heeger (1994) and Carandini et al. (1997) is based on normalization of neural response operated by divisive inhibition. This model also predicts a phase advance with contrast that simulates well the striate neural response in monkey. The delay varies with temporal frequency, from about 20 ms at 13 Hz to about 100 ms at 1.6 Hz. The delays observed at both the subcortical and cortical level in monkeys are similar to those observed for both cat (Morrone et al., 1987; Morrone, Burr, & Speed, 1991) and human VEP (Burr & Morrone, 1987) and observed here for luminance and chromatic VEP data. Interestingly, applying Shapley and Victor's model (equation 1 of Shapley & Victor, 1981) with their average measured increase of the constants of the feedback loop ($k\tau$ from 2 to 20 ms in 1 log-unit of contrast) and using seven stages of the feedback loop, it is possible to model accurately both the saturation of the amplitude response curve and the phase advance over 2π rad/log-units of contrast at a frequency of 16 Hz. The use of a cascade of seven stages is suggestive of a gain control that is exerted at several levels, from retina to cortex. A VEP study in cat primary cortex supports the view of several stages, showing that, during local block of GABAergic inhibition, the phase advance is greatly reduced and the amplitude multiplicatively increased (Morrone et al., 1987).

Attention reduced the phase advance with luminance contrast. Within the framework of the Shapley and Victor model, this implies that the feedback integration

time changes less with stimulus contrast; within the normalization model, it implies a change of the integration constant of the membrane. A small reduction of the parameter $k\tau$ of the above simulation by a factor 0.7 is able to model simultaneously the effect of attention on amplitude and on phases, reducing gain by a factor of 1.4 and phase advance by 0.6π rad/log-unit of contrast. Reducing the feedback stages from 7 to 5 can simulate equally well the attentional effects, without directly control the temporal constant. In both cases, the advantage of setting alteration of the feedback loop by attention is to reduce processing time for low contrast stimuli, using mechanisms already in place for other purposes. The observed decrement of about 10 ms/log-unit contrast is consistent with the acceleration of processing time measured by transient VEPs and estimated from steady-state VEPs at various temporal frequencies (Di Russo & Spinelli, 1999a).

The contrast gain mechanism acting through a feedback loop seems to occur exclusively in the magno-cellular pathway (Bernardete & Kaplan, 1999; Bernardete et al., 1992; Lee et al., 1994). Only these types of cells change their latency and temporal tuning with contrast, while parvo-cell latency and temporal tuning remain constant in response to both isoluminant and luminance modulated stimuli (Bernardete et al., 1992; Lee et al., 1994). Unfortunately, at present, no single-cell data are currently available for cortical response to equiluminant stimuli. Our data, consistent with previous data, indicate that also the human VEP chromatic responses are subject to contrast gain control, probably only at the cortical level, although other interpretations are equally possible. For instance, different sources with different integration times may contribute to the VEP response, and their relative contribution may vary with contrast. However, whatever the explanation of the phase advance for isoluminant grating, attention did not cause a systematic change in it. This result points to a possible difference between the attentive control operating for the colour and luminance cortical mechanisms.

It is interesting to compare the present luminance data with those obtained in masking VEP experiments, where contrast–response curves were measured in the presence of parallel or orthogonal luminance-modulated stimuli (Morrone & Burr, 1986; Morrone et al., 1987; Burr & Morrone, 1987). A superimposed mask grating orientated orthogonal to the test grating attenuates VEP amplitudes multiplicatively (so-called cross-orientation inhibition) and increases the phase advance. The effect of the mask mimics the attention engagement on another task (unattended condition) for both VEP amplitude and phase. It has been proposed that orthogonal masking effects on VEP are mediated by the automatic contrast gain control mechanisms previously described. Attention may use the same inhibitory cir-

cuitry already in place for contrast regulation to increase the efficiency in processing time and in contrast discriminability. This has the advantage of improving vision without imposing any additional cost of a specific circuitry devoted to attentional resources.

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References

- Angeles, P., De Luca, M., & Spinelli, D. (1996). Early visual processing in neglect patients: a study with steady state VEPs. *Neuropsychologia*, *34*, 1151–1157.
- 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.
- Bernardete, E. A., & Kaplan, E. (1999). The dynamics of primate M retinal ganglion cells. *Visual Neuroscience*, *16*, 355–368.
- Bernardete, E. A., Kaplan, E., & Knight, B. W. (1992). Contrast gain control in the primate retina: P cells are not X-like, some M cells are. *Visual Neuroscience*, *8*, 483–486.
- Bonds, A. B. (1989). Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex. *Visual Neuroscience*, *2*, 41–55.
- Boynton, G. M., Demb, J. B., Glover, G. H., & Heeger, D. J. (1999). Neuronal basis of contrast discrimination. *Vision Research*, *39*, 257–269.
- Burr, D. C., & Morrone, M. C. (1987). Inhibitory interactions in the human visual system revealed in pattern visual evoked potentials. *Journal of Physiology (London)*, *389*, 1–21.
- Burr, D. C., & Morrone, M. C. (1996). Temporal impulse response functions for luminance and colour during saccades. *Vision Research*, *36*, 2069–2078.
- Campbell, 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.
- Carandini, M., & Heeger, D. J. (1994). Summation and division by neurons in primate visual cortex. *Science*, *264*, 1333–1335.
- Carandini, M., Heeger, D. J., & Movshon, J. A. (1997). Linearity and normalization in simple cells of the macaque primary visual cortex. *Journal of Neuroscience*, *17*, 8621–8644.
- Carrasco, M., Pempeci-Talgar, C., & Eckstein, M. (2000). Spatial covert attention increases contrast sensitivity across the CSF; support for signal enhancement. *Vision Research*, *40*, 1203–1216.
- Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discrimination of shape, color and speed; functional anatomy by positron emission tomography. *Journal Neuroscience*, *11*, 2383–2402.
- Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 219–240.
- Di Russo, F., & Spinelli, D. (1999a). Electrophysiological evidence for an early attentional mechanism in visual processing in humans. *Vision Research*, *39*, 2975–2985.
- Di Russo, F., & Spinelli, D. (1999b). Spatial attention has different effects on the magno- and parvo-cellular pathways. *NeuroReport*, *10*, 2755–2762.
- Downing, C. (1988). Expectancy and visual-spatial attention: effects on perceptual quality. *Journal of Experimental Psychology: Human Perception and Performance*, *14*, 188–202.
- Fiorentini, A., Burr, D. C., & Morrone, M. C. (1991). Temporal characteristics of colour vision: VEP and Psychophysical measurements. In A. Valberg, & B. B. Lee, *From pigment to perception* (pp. 139–149). New York: Plenum Press.
- Foley, J. M., & Schwarz, W. (1998). Spatial attention: effect of position uncertainty and number of distractor patterns on the threshold-versus-contrast function for contrast discrimination. *Journal of the Optical Society of America*, *15*, 1036–1047.
- Gandhi, S. P., Heeger, D. J., & Boynton, G. M. (1999). Spatial attention affects brain activity in human primary visual cortex. *Proceedings of the National Academy of Sciences USA*, *16*, 3314–3319.
- He, S., Cavanagh, P., & Intrilligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*, 334–337.
- 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: Massachusetts Institute of Technology.
- Lee, B. B., Pokorny, J., Smith, V. C., & Kremers, J. (1994). Responses to pulses and sinusoids in macaque ganglion cells. *Vision Research*, *34*, 3081–3096.
- Lee, B. B., Pokorny, J., Smith, V. C., Martin, P. R., & Valberg, A. (1990). Luminance and chromatic modulation sensitivity of macaque ganglion cells and human observers. *Journal of Optical Society of America A*, *7*, 2223–2236.
- Lee, D. K., Itti, C., & Braun, J. (1999). Attention activates winner-take-all competition among visual filters. *Nature Neuroscience*, *2*, 375–381.
- Lee, D. K., Koch, C., & Braun, J. (1997). Spatial vision threshold in the near absence of attention. *Vision Research*, *37*, 2409–2418.
- Lu, Z., & Doshier, B. A. (1998). External noise distinguishes attention mechanisms. *Vision Research*, *38*, 1198–1199.
- McAdams, C. J., & Maunsell, J. H. R. (1999). Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4. *The Journal of Neuroscience*, *19*, 431–441.
- Martinez, A., Anillo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., Wong, E. C., Hinrichs, H., Heinze, H. J., & Hillyard, S. A. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*, 364–369.
- Merigan, W. H. (1989). Chromatic and achromatic vision of macaques: role of the P pathway. *Journal of Neuroscience*, *9*, 776–783.
- Morrone, M. C., & Burr, D. C. (1986). Evidence for the existence and development of visual inhibition in humans. *Nature*, *321*, 235–237.
- Morrone, M. C., Burr, D. C., & Speed, H. (1987). Cross-orientation inhibition in cat is GABA mediated. *Experimental Brain Research*, *67*, 635–644.
- Morrone, M. C., Burr, D. C., & Fiorentini, A. (1993). Development of infant contrast sensitivity to chromatic stimuli. *Vision Research*, *17*, 2535–2552.
- Morrone, M. C., Burr, D. C., & Maffei, L. (1982). Functional significance of cross-orientation inhibition. Part I, Neurophysiology. *Proceedings of the Royal Society of London, Series B*, *216*, 335–354.
- Morrone, M. C., Burr, D. C., & Speed, H. (1991). Development of visual interactions in kittens. *Visual Neuroscience*, *7*, 321–334.
- Muller, H. J., & Findlay, J. (1987). Sensitivity and criterion effects in the spatial cueing of visual attention. *Perception & Psychophysics*, *42*, 393–399.
- Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, *29*, 1631–1647.

- Pashler, H. E. (1998). *The psychology of attention*. Cambridge, MA: MIT Press.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.
- Reid, R. C., Victor, J. D., & Shapley, R. M. (1992). Broadband temporal stimuli decrease the integration time of neurons in cat striate cortex. *Visual Neuroscience*, *9*, 39–45.
- Sclar, G. (1987). Expression of 'retinal' gain control by neurons of the cat's lateral geniculate nucleus. *Experimental Brain Research*, *66*, 589–596.
- Sengpiel, F., & Hubener, M. (1999). Visual attention: spotlight on the primary visual cortex. *Current Biology*, *9*, 318–321.
- 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.
- Shapley, R. M., & Victor, J. D. (1979). Nonlinear spatial summation and the contrast gain control of cat retinal ganglion cells. *Journal of Physiology (London)*, *290*, 141–161.
- Shapley, R. M., & Victor, J. D. (1981). How the contrast gain control modifies the frequency responses of cat retinal ganglion cells. *Journal of Physiology (London)*, *318*, 161–179.
- Shaw, M. L. (1984). Division of attention among spatial locations: a fundamental difference between detection of letters and detection of luminance increments. In H. Bouma, & D. G. Bowhuis, *Attention and performance*, vol. 10 (pp. 109–121). Hillsdale, NJ: Erlbaum.
- Smith, V. C., & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research*, *15*, 161–171.
- Somers, D. C., Dale, A. M., Seiffert, A. E., & Tootell, R. B. (1999). Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proceedings of the National Academy of Sciences USA*, *96*(4), 1663–1668.
- 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*, 553–556.
- 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.
- Titchener, E. B. (1908). *Lectures on the elementary psychology of feeling and attention*. New York: Macmillan.
- Tootell, R. B., Hadjikhani, N., Hall, E. K., Marrett, S., Vanduffel, W., Vaughan, J. T., & Dale, A. M. (1998). The retinotopy of visual spatial attention. *Neuron*, *21*, 1409–1422.
- Treue, S., & Martinez, J. C. (1998). Attentional modulation of direction-selective responses in MT/MST resembles the effect of reducing contrast of unattended stimuli. *Society of Neuroscience Abstract*, *24*, 1249.
- Treue, S., & Maunsell, J. H. R. (1999). Effect of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *Journal of Neuroscience*, *19*, 7591–7602.
- Victor, J. D., & Shapley, R. M. (1979). Receptive field mechanisms of cat X and Y retinal ganglion cells. *Journal of General Physiology*, *74*, 275–298.
- Watanabe, T., Sasaki, Y., Miyauchi, S., Putz, B., Fujimaki, N., Nielsn, M., Takino, R., & Miyakawa, S. (1997). Attention-regulated activity in human primary visual cortex. *Journal Neurophysiology*, *79*, 2218–2221.
- Watanabe, T., Harner, A. M., Miyauchi, S., Sasaki, Y., Nielsen, M., Palomo, D., & Mukai, I. (1998). Task-dependent influences of attention on the activation of human primary visual cortex. *Proceedings of the National Academy of Science*, *95*, 11489–11492.
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs isual performance by enhancing spatial resolution. *Nature*, *396*, 72–75.