NeuroReport 10, 2755–2762 (1999)

Spatial attention has different effects on the magno- and parvocellular pathways

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ATTENTION was directed to the left or to the right of the fixation point by the lateral presentation of a target on which the subject had to perform an attention demanding task. A (task-irrelevant) grating displayed in the left visual field was the visual evoked potential (VEP) stimulus. Gratings modulated either in luminance or colour contrast at various temporal frequencies were used in order to maximise the activation of magno- or parvocellular pathways. VEPs recorded in attended and unattended conditions were compared. For luminance stimuli, both latency and amplitude of VEPs were modified by attention. For chromatic stimuli, attention affected the amplitude but not the latency of VEPs. Spatial attention uses different mechanisms when magno- or parvocellular systems are involved. *NeuroReport* 10:2755–2762 © 1999 Lippincott Williams & Wilkins.

Key words: Colour; Latency; Luminance; Spatial attention; Steady state; Visual evoked potentials

Introduction

It is widely accepted that attention enhances the amplitude of sensory responses to stimuli (for review see [1]). However, it has been shown recently that, associated with this amplitude enhancement, attention also affects the VEP latency [2]. The processing speed of the visual stimuli localised in the attended space is faster. This suggests that the neural mechanism of attention operates to give priority to stimuli in the selected space. In that experiment [2] the effect on latency was larger with steady state than with transient stimulation. This may reflect a major involvement of the magnocellular pathway with high temporal frequency steady-state stimulation. Thus, it might be hypothesised that the mechanism responsible for priority to stimuli in the attended space relies on the fast transmission magnocellular pathway.

The present study investigates this hypothesis by comparing the effect of spatial attention on VEPs recorded for luminance and chromatic stimuli. Although this may not segregate totally the magnocellular and parvocellular systems, the stimuli used in the present study should maximise the segregation. The experiment examined whether amplitude enhancement and shortening of latency observed for luminance stimuli as a consequence of spatial attention was also present for chromatic patterns.

Materials and Methods

VEPs were recorded in responses to a grating (a task-irrelevant background) displayed continuously in the left hemifield. The target was a red LED turning on and off, superimposed on the grating in the attended condition or on a grey background in the right hemifield in the unattended condition. The subject was instructed to covertly orient his/her attention towards the side where the LED was active. Thus, the experiments compared the visual responses evoked by the stimulus located in the left side when attention was directed to this portion of space or to the opposite side.

Subjects: Four subjects (two males and two females; mean age 28 years) with normal or corrected to normal vision participated in the study; all were trained observers and informed about the general purpose of the experiment in order to obtain the maximum reliability in the fixation task.

Stimuli: A cross in the centre of the display served as fixation point. The stimulus was a horizontal sinusoidal 1 c/deg grating, 19° wide and 16° high. The grating was displayed in the left visual field (LVF), 1.5° to the left of the fixation point. A grey area was displayed in the right visual field (RVF). The stimuli were modulated either in luminance

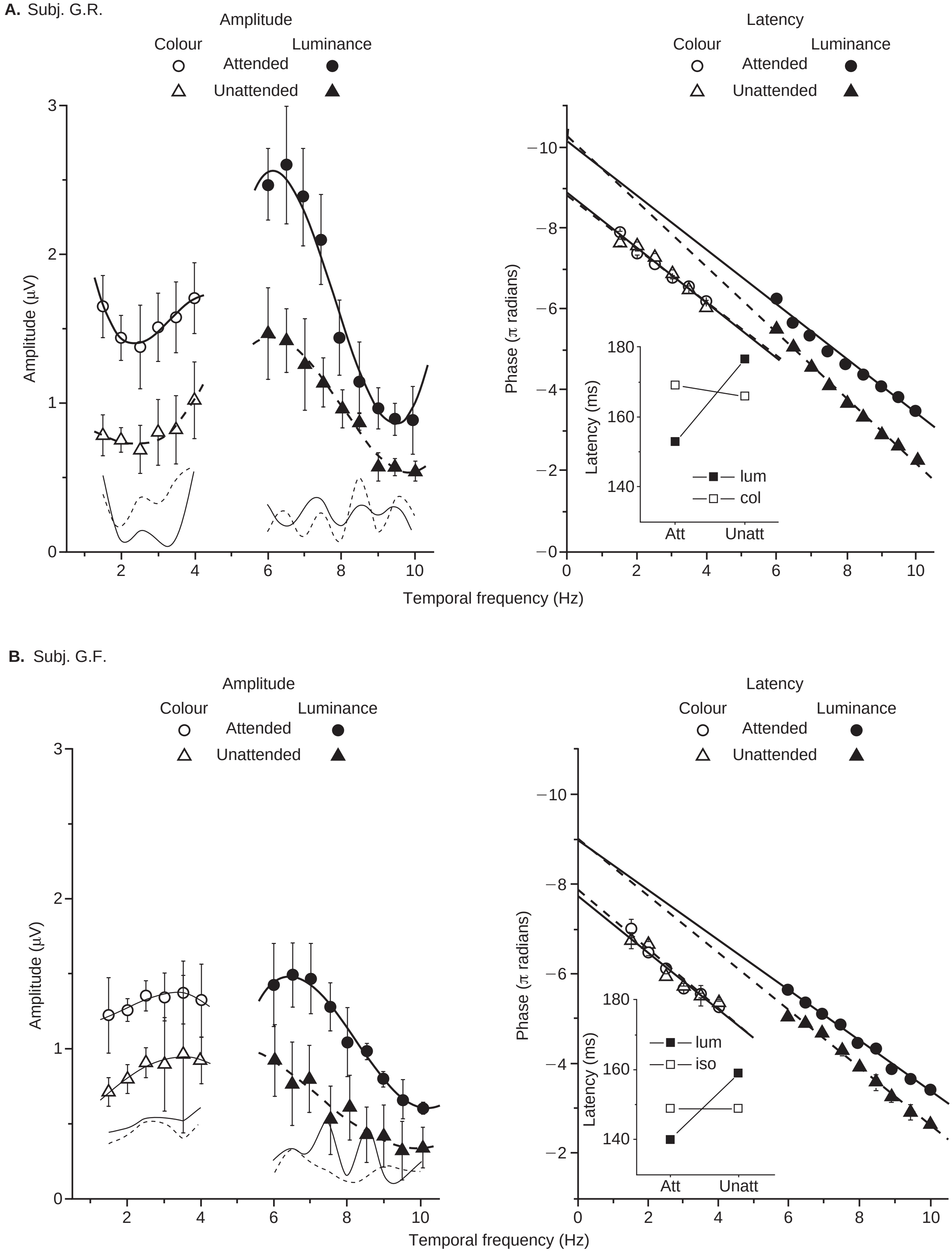
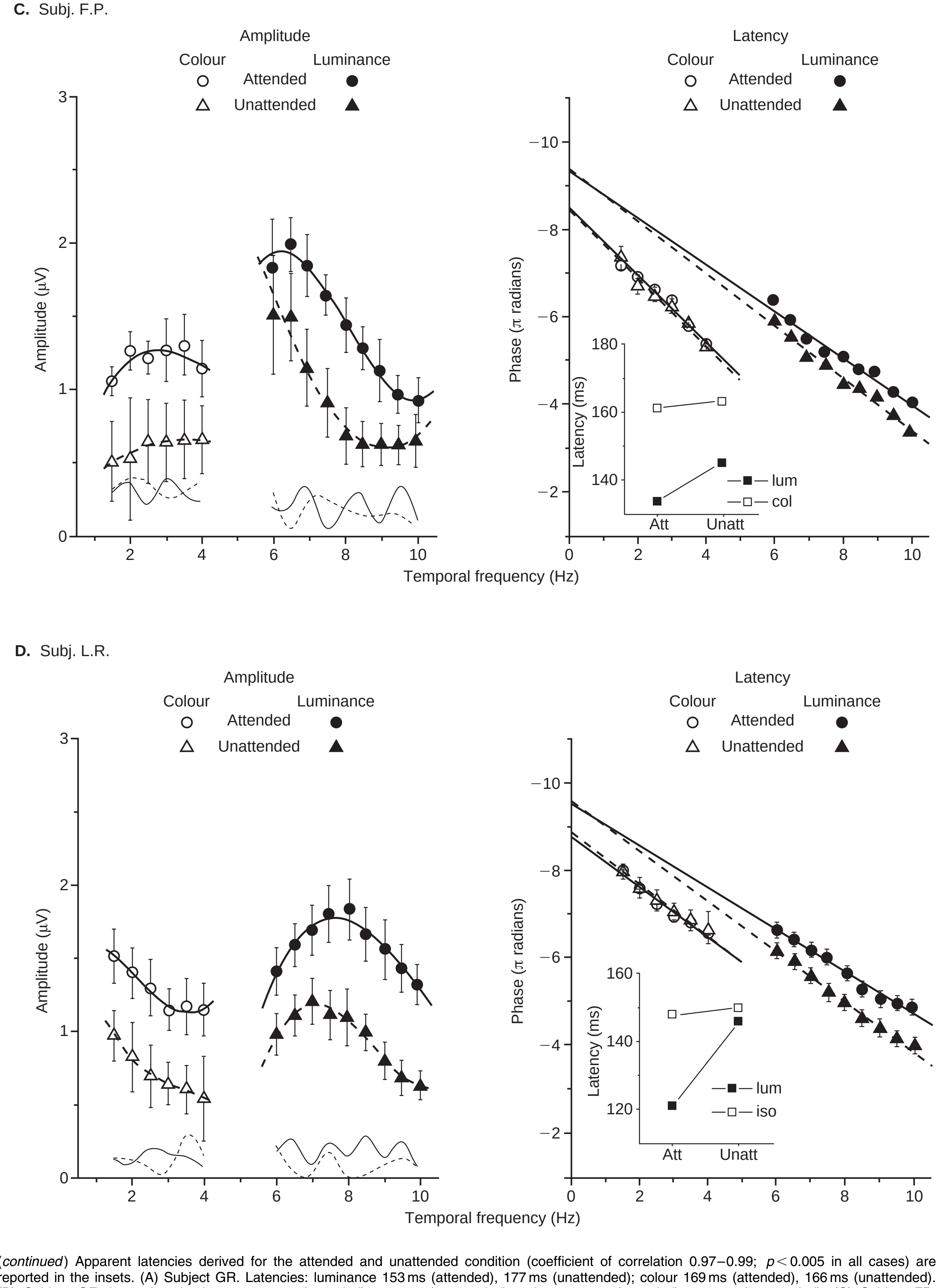


FIG. 1. The effect of attention on VEPs for luminance and chromatic gratings. Data from four subjects are reported in the (**A–D**). Left part of the figure: VEPs amplitude and standard errors are reported as a function of temporal frequency. Filled symbols: luminance gratings. Open symbols: isoluminant gratings. The attended condition is reported with circles, the unattended condition by triangles. Noise level in the two conditions is also reported with continuous and dashed thin lines. Right part of the figure: VEPs phases in pi radians are reported as a function of the temporal frequency. Note the difference in phases between the attended and unattended responses for luminance gratings and the absence of difference for chromatic gratings.

(*continued overleaf.*)



(*continued*) Apparent latencies derived for the attended and unattended condition (coefficient of correlation 0.97–0.99; $p < 0.005$ in all cases) are reported in the insets. (A) Subject GR. Latencies: luminance 153 ms (attended), 177 ms (unattended); colour 169 ms (attended), 166 ms (unattended). (B) Subject GF. Latencies: luminance 140 ms (attended), 159 ms (unattended); colour 149 ms (attended), 149 ms (unattended). (C) Subject FP. Latencies: luminance 134 ms (attended), 146 ms (unattended); colour 163 ms (attended), 165 ms (unattended). (D) Subject LR. Latencies: luminance 121 ms (attended), 146 ms (unattended); colour 148 ms (attended), 150 ms (unattended).

(yellow–black) or in chromaticity (red–green). For the luminance condition, the contrast of the grating (20%) was reversed sinusoidally at temporal frequencies between 6 and 10 Hz; for the colour condition, the contrast of the grating (80%) was reversed between 1.5 and 4 Hz. The nominal chromatic contrast roughly equates the effective cone excitation to that of the luminance contrast condition (e.g. [3]). 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 [4]. In the colour study the equiluminant point was preliminarily evaluated for each subject according to a flicker photometry procedure. The ratio of red to total luminance (r = red/red + green) could be varied from 0 to 1. Red–green gratings were sinusoidally reversed at 16 Hz and the r ratio was varied to null or minimise the perception of flicker. The equiluminance point was close to 0.5 in all subjects (range 0.49–0.52). Two LEDs were mounted on the display 8.5° to the left and to the right of the fixation point. To draw attention, one of the two LEDs was turned on and off at a random rate. Occasionally the on duration was longer.

Procedure: The subject, seated in a dimly lit room 100 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 LED and count the number of rare long-duration onsets. Two main conditions were studied. In the attended condition (condition 1) the target was in the LVF, superimposed on the grating, while in the unattended condition (condition 2) the target was in the RVF. 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. A preliminary experiment showed that the presence of the lighting LED *per se* did not affect the latency or the amplitude of the VEP (see also [2], Fig. 7). When the subject felt ready, he pressed a hand-held key to start the recording. Each VEP was evoked by 200–300 stimulus repetitions. A short pause (30 s) was given after each run. The subject could interrupt recording if he/she felt uncomfortable (by releasing the key). The temporal frequency varied from lower to higher values; a short pause was given after each run (200–300 stimulus repetitions). Long intervals (2–3 min) were given between attended and unattended trials (presented in two separate blocks). The order of blocks was balanced across subjects. Two subjects were submitted to luminance and colour testing in the same session (about 1.5 h); two other subjects were tested in two different sessions (one for luminance and one for colour).

VEP recording and data analysis: Steady-state 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 [5]. Phase changes with temporal frequency and apparent latency may be derived [6,7]. The method used was developed by Burr and Morrone in various studies (e.g. [8,9]). On-line Fourier analysis was performed to calculate the amplitude and the phase of the second harmonic component. The electrical signals at a temporal frequency near that of the stimulus but not synchronously with it were also averaged. 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. VEP phases were plotted as a function of temporal frequency and regression line was calculated. The slope of the regression line was calculated by least-squares fit, after weighting each data point by its signal-to-noise ratio. The latency was estimated from the slope of the regression line.

Results

In all cases the number of long-onset targets was reported correctly by the subjects, confirming that their attention was effectively directed toward the target. VEP amplitudes, phase data and derived apparent latencies of the four subjects are reported in Fig. 1A–D for both luminance and colour.

The amplitude enhancement by attention is evident in both cases. On the other hand, data diverge for what regard latencies. In all subjects latencies were shorter in the attended condition than in the unattended one but only for luminance stimuli (latency differences were 24, 19, 12 and 25 ms for GR, GF, FP and LR, respectively). When chromatic stimuli were used, the two regression lines of phases against temporal frequency had the same slope. The apparent latency in the attended *vs* unattended condition was 169 ms *vs* 166 ms, 149 ms *vs* 149 ms, 163 ms *vs* 165 ms and 148 ms *vs* 150 ms for GR, GF, FP and LR, respectively.

Data were submitted to separate ANOVAs. For amplitude, only the effect of attention was significant ($F(1,2) = 89.84$; $p < 0.0025$). For latency, the interaction between effect of attention and type of stimulus was significant ($F(1,2) = 18.31$; $p < 0.05$). The mean latency difference between attended and unattended conditions was 20 ms for luminance ($p < 0.05$) and 1 ms for colour (n.s.).

The right part of Fig. 2 replots latency data (separately for luminance and colour) with values obtained in the attention condition against those measured without attention. The dotted line indicates equal latency for attended and unattended responses. Data from the colour condition fit this trend. The fit by a linear equation was very good (coefficient of correlation 0.98) and the slope was 1.05. On the other hand, for luminance, the latencies were shorter in the attended conditions (all points fell below the equilatency line). In this case the slope was 0.74 (coefficient of correlation 0.88). Thus, VEP latency were virtually unaffected by attention in the case of chromatic grating, while attention decrease latencies in the case of luminance gratings.

The phase differences between attended and unattended condition were also calculated for each temporal frequency for luminance and colour conditions. Data are summarised in Fig. 3. The phase shift was consistent across temporal frequencies for luminance stimuli (e.g. phases to attended stimuli were consistently advanced or retarded with respect to the unattended ones). Moreover, the phase shift produced by attention showed a tendency to be

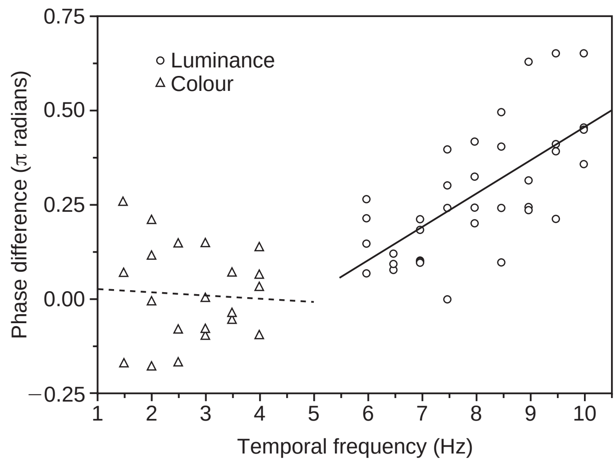


FIG. 3. The phase differences between attended and unattended condition. For luminance stimuli the phase shift produced by attention was consistent across temporal frequency and was more marked at higher temporal frequencies (continuous line: $y = -0.43 + 0.09x$; $R = 0.69$). The phase shift was inconstant and independent from temporal frequency in the case of chromatic stimuli ($y = 0.03 - 0.008x$; $R = -0.058$).

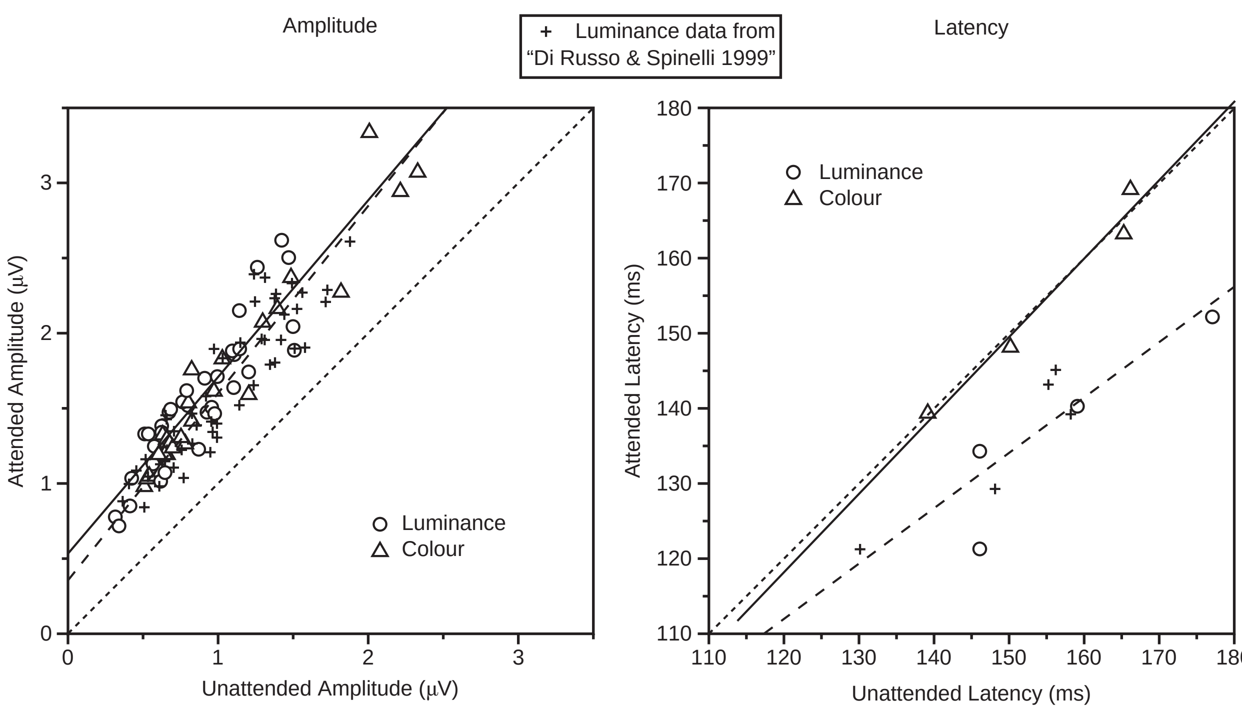


FIG. 2. Scatterplots of individual data from Fig. 1A–D. Right part of the figure: latency of attended *vs* unattended stimuli. The dotted line indicates equilatency for attended and unattended VEP. Data from the chromatic pattern (triangles) fit this trend (continuous line: $y = -7.5 + 1.04x$; $R = 0.99$). For luminance (circles; dashed line: $y = 22.9 + 0.74x$; $R = 0.88$), the latencies were shorter in the attended conditions (all values below the equilatency line). Data from a previous study [2] are indicated by crosses. Left part of the figure: amplitude enhancement due to attention. The dotted line indicates equal amplitude for attended and unattended VEP. Data from both chromatic (dashed line: $y = 0.35 + 1.30x$; $R = 0.98$) and luminance (continuous line: $y = 0.52 + 1.18x$; $R = 0.89$) patterns showed larger amplitude in the attended conditions (all values above the dotted line). When also crosses are fitted by linear equation, the slope for luminance is 1.2.

slightly larger at higher temporal frequencies (slope 0.09; coefficient of correlation 0.69). On the other hand data from colour condition do not show any systematic trend, phase shift was inconstant and independent from temporal frequency (coefficient of correlation −0.058; n.s.).

To quantify the nature of the amplitude enhancement by attention, individual data obtained at all temporal frequencies were replotted in the left part of Fig. 2. In this figure the amplitudes measured with attention are plotted against those measured without attention. The best linear estimate of the relationship was calculated by least square fit, after the data had been weighted by their reliability (signal to noise ratio) separately for luminance and colour condition. The linear coefficient of the fitted equation provides an estimate of the multiplicative factor. Both luminance and colour data were fitted by linear equations (coefficients of correlation 0.89 and 0.98), with slopes 1.18 and 1.30 for luminance and colour, respectively. While signal amplitude showed a clear enhancement by attention in all cases, the amplitude of noise (measured as indicated in Materials and Methods) did not vary much. In the attended condition noise was slightly larger than in the unattended condition (0.23 *vs* 0.17 μV; $t = 2.97$, $p < 0.01$) for luminance stimuli and comparable in the case of colour (0.30 *vs* 0.32 μV; $t = -1.05$, n.s.).

Control experiment: In the above experiments eye movements were controlled only through a camera by the experimenter. All subjects were trained observers and started and interrupted the trial at will through the hand held key. Lapses of gaze were rare and should have had a presumably small effect on the averaged VEP (200–300 sums). However, the present experiment was designed to measure the effect of small eccentricity variations, such as those possibly produced by a gaze shift in the direction of the grating.

The grating was displayed in the LFV and the subject's task was to hold his gaze on the fixation point, which was displaced towards the grating in different trials. This control experiment was done with coloured stimuli in two subjects (Fig. 4) and with luminance stimuli in one subject (Fig. 5). When the fixation point was shifted toward the grating, a clear enhancement occurred for both luminance and chromatic stimuli. For latency, however, there was a difference between the two conditions. Phase variation and derived apparent latencies are reported in the right part of the figures. With luminance the latency variations had a small-size and did not show a trend in the direction of the shortening of the latency (confirming earlier observations [2]). On the other hand, with colour, there was a progressive shortening of latency when the fixation point was moved towards the grating. When the entire fovea was involved (−2° on the abscissa), latency was about 135 ms, a value comparable to those reported in the literature for similar conditions [9]. Thus, if the eyes move towards the chromatic pattern (as in the control experiment) the latency changes. However, latency does not change in the attention experiment with chromatic pattern as described above. On the other hand, when the eyes move towards the luminance grating, the latency does not become shorter as it does in the attention experiment. Overall, this implies that the effect of attention above described cannot be due to a spurious effect of eye movements.

Discussion

There is a debate about the degree of separation between magnocellular and parvocellular pathways (for review see [10]). Although recent studies suggest that segregation is not complete [11] it is generally agreed that equiluminance [12] and low temporal frequencies [13] favour parvocellular activity. In the present study equiluminance low temporal frequency stimuli were contrasted with luminance high temporal frequency stimuli with the aim of maximizing the segregation between the two pathways. Under the assumption that the two types of stimuli used were apt to privilege magno- and parvocellular activity, the present study indicates that attention acts in a different way on the two neural substrates.

Although VEP amplitude was enhanced by attention in all cases, the phase advance with temporal frequency, and the derived apparent latency, was changed only for luminance stimuli. In this case attention shortened the latency to stimuli displayed in the attended visual field.

Latency gives a measure of the temporal integration period, only a small part of the latency being due to transmission time [14,15]. Thus, we might assume that attention acts on the magnocellular stream through a decrement of the temporal integration time. Neurons seem to be able to respond more quickly to the stimuli in the attended portion of space. On the other hand, attention seems to acts through a different mechanism in the parvocellular stream, where integration time does not change.

Attention might act at least in two ways. On the one hand, more resources might be allocated to stimuli at the cued location. The increment of VEP amplitude observed in all cases is consistent with this idea. On the other hand a priority order might be established. The shortening of VEP latencies to

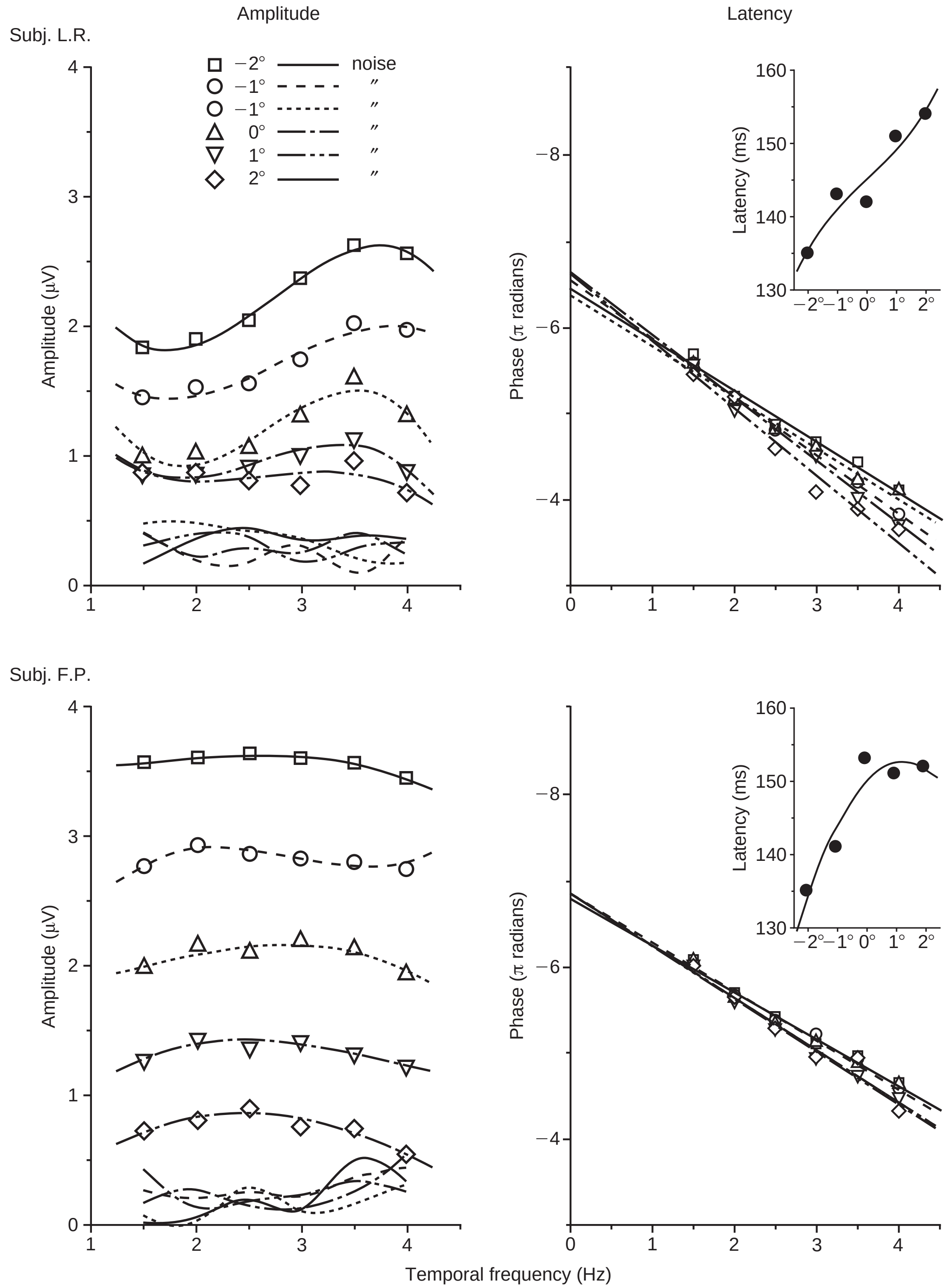


FIG. 4. Control experiment on the effect of eye movements for chromatic gratings. The amplitude and the latency data at the various fixation point positions (in degrees) are reported for two subjects. The eccentricity used in the attention experiment (1.5° from the edge of the grating) corresponds to value zero in this plot (upright triangles). Negative values indicate displacements of the fixation point towards the left, i.e. towards the grating. At −2° the fixation point was superimposed on the grating and the entire fovea was activated. Note the increment of amplitude (on the left) and the systematic shortening of the latency (on the right) with the change in location of the fixation point. While the increase in amplitude due to eye movements might be compatible with that produced by attention, the progressive shortening of the latency associated to less eccentric fixation was absent in the attention experiment.

luminance background stimuli at the cued location is congruent with this view. Present data indicate that the attention mechanisms responsible for priority order rely on the magnocellular pathway. The notion that the magnocellular system is the quickest pathway of the visual system fits with the idea that it is devoted to signal processing priority. Thus, we can propose that in the real environment where

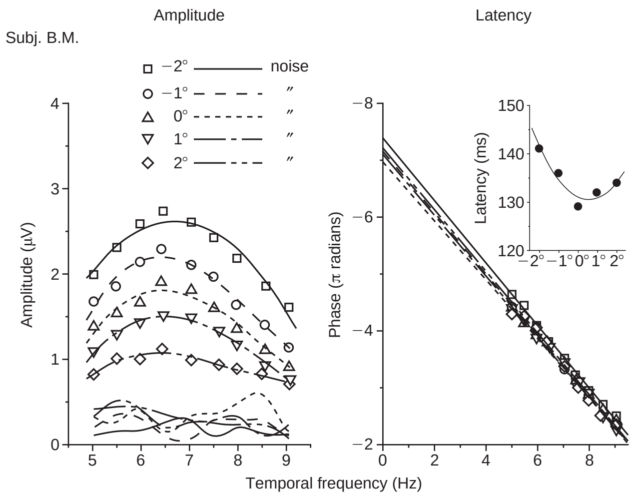


FIG. 5. Control experiment on the effect of eye movements for luminance gratings. The amplitude and the latency data at the various fixation point positions are reported for one subject. Symbols as in Fig. 4. In the case of luminance gratings the increment of amplitude (on the left) was not associated with a shortening of the latency (on the right). While the increase in amplitude due to eye movements might be compatible with that produced by attention, the absence of a shortening trend in the latency diverges from attentional data, were clear shortening of latency was shown.

isoluminant stimuli are rare, the activation of the magnocellular system would direct resource allocation through a fast sensory signal, triggering enhancement of activity of both subsystems.

This view is supported by studies on patients with attention deficits. These patients neglect contralesional stimuli. Electrophysiological studies have shown specific damage to magnocellular pathway devoted to signal contralesional luminance stimuli in these patients [16,17]. The specific involvement of the magnocellular stream in visual attention is also supported by a study showing that cues that preferentially excite the magnocellular pathway predominantly capture visual attention [18].

Conclusion

Attention towards a portion of space produces an enhancement of visual activity. This is associated with a shortening of latencies for luminance stimuli but not for chromatic stimuli. It is proposed that, through the fast signals of the magno-cellular subsystem, attention gives priority to stimuli in the attended space, directing resource allocation and triggering enhancement of activity of the other subsystem.

References

1. Hillyard SA, Mangun GR, Woldorff MG and Luck SJ. Neural systems mediating selective attention. In: Gazzaniga MS, ed. *The Cognitive Neurosciences.* Boston: Massachusetts Institute of Technology, 1995: 665–681.
2. Di Russo F and Spinelli D. *Vision Res* **39**, 2975–2985 (1999).
3. Morrone MC and Bedarida L. A model of cone interaction for coding chromatic information. In: Dickinson C, ed. *Colour Vision Research: Proceedings of the John Dalton Conference 9–13 September 1994.* London: Taylor and Francis (1995).
4. Morrone MC, Burr DC and Fiorentini A. *Vision Res* **17**, 2535–2552 (1993).
5. Campbell FW and Maffei L. *J Physiol (Lond)* **192**, 345–358 (1970).
6. Regan D. *EEG and Clinical Neurophysiol* **20**, 238–248 (1966).
7. Spekreijse H, Estevez O and Reits D. Visual evoked potentials and the physiological analysis of visual processes in man. In: Desmedt JE, ed. *Visual Evoked Potentials in Man: New Developments.* Oxford: Clarendon Press, 1977: 16–89.
8. Porciatti V, Burr DC, Morrone MC and Fiorentini A. *Vision Res* **32**, 1199–1209 (1992).
9. Morrone MC, Fiorentini A and Burr DC. *Vision Res* **36**, 3141–3155 (1996).
10. Merigan WH and Maunsell JHR. *Annu Rev Neurosci* **16**, 369–402 (1993).
11. Victor JD, Purpura KP and Conte MM. *Vis Neurosci* **15**, 607–624 (1998).
12. Merigan WH. *J Neurosci* **9**, 776–783 (1989).
13. Derrington AM and Lennie P. *J Physiol (Lond)* **357**, 219–240 (1984).
14. Shapley RM and Victor JD. *J Physiol (Lond)* **285**, 275–298 (1981).
15. Reid RC, Victor JD and Shapley RM. *Vis Neurosci* **9**, 39–45 (1992).
16. Spinelli D, Angelelli P, De Luca M and Burr CD. *Neuroreport* **7**, 815–819 (1996).
17. Doricchi F, Angelelli P, De Luca M and Spinelli D. *Neuroreport* **7**, 1360–1364 (1996).
18. Steinman BA, Steinman SB and Lehmkuhle S. *Vision Res* **37**, 17–23 (1997).

ACKNOWLEDGEMENTS: We are grateful to David Burr and Concetta Morrone for providing us with their VEP software and for comments on the manuscript.

Received 17 June 1999; accepted 6 July 1999