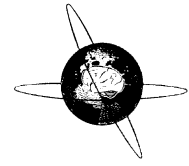




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Perception of static eye gaze direction facilitates subsequent early visual processing

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Abstract

Objective: Using event-related potentials (ERPs), it has been recently shown that a reflexive shift of attention following the observation of a dynamic eye gaze cue enhances and speeds up early visual processing of a target presented at the gazed-at location. Here we investigate whether similar early sensory modulations are also elicited by static gaze cues, or if previously described attentional effects were caused mainly by visual motion cues and not by eye gaze direction per se. Furthermore, we explore if these possible attentional orienting effects reflect facilitation of the processing of cued stimuli, inhibition of the unattended stimuli, or both.

Methods: Subjects were presented with a face looking to the right or left visual field (VF), or straight away, before the occurrence of a lateralized target to detect. There were 3 conditions in this nonpredictive cueing task: (1) target presented in the VF indicated by the eye gaze direction (congruent); (2) opposite to the eye gaze direction (incongruent); or (3) preceded by a straight gazing face (neutral).

Results: Subjects were faster at detecting congruently than incongruently and neutrally cued targets. Facilitation effects were observed on early ERP components: the occipital P1 and occipito-temporal N1 components were speeded up as early as ~100 ms following stimulus onset (P1), and enhanced (P1 and N1) in response to congruent trials, particularly in the right hemisphere.

Conclusions: Spatial attention triggered by static eye gaze direction produces response facilitations – predominantly lateralized to the right hemisphere – from the early sensory stages of visual processing.

Significance: This study provides the first evidence of a speeding up and amplification of early visual processing following attention triggered by static eye gaze perception.

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Keywords: Visual-spatial; Selective attention; Visual processing; Eye gaze

1. Introduction

Direction of eye gaze is an important indicator of another individual's focus of attention (Kleinke, 1986). Recent behavioural studies showed that another person's eye gaze and head position shifts automatically the observer's attention in the direction indicated by these cues (Friesen and Kingstone, 1998; Driver et al., 1999; Hietanen, 1999; Langton and Bruce, 1999). Precisely, lateralized targets are detected faster when a central face is gazing in the direction of a target location (congruent trials) than when the eyes are directed to the opposite site (incongruent trials). This shifting of spatial attention is observed even though the gaze

direction is not predictive of the location of the forthcoming target. Recently, event-related potentials (ERPs) were used to investigate the time-course of this special attentional orienting triggered by eye gaze (Schuller and Rossion, 2001). In that study, scalp ERPs were measured on human subjects while they detected a lateralized target whose location was cued by a dynamically averted eye gaze. In agreement with ERP studies of visual spatial attention (for a review see Luck et al., 2000), it was observed that visual extrastriate P1 (~120 ms) and N1 (~170 ms) components in response to the lateralized targets were amplified when preceded by a congruent gaze direction. Moreover, the peak latency of these components was shorter in the congruent condition, suggesting that eye gaze can also speed up the visual processing of attended items (Schuller and Rossion, 2001). This finding contrasts with the observation that attentional effects on early visual components, as observed

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in predictive, symbolic cueing (e.g. arrows, Luck et al., 1994) or sustained attentional paradigms (e.g. Hillyard and Anllo-Vento, 1998), are generally characterized by amplitude modulations only (e.g. Luck et al., 2000) (although see Di Russo and Spinelli, 1999; Di Russo et al., 2001). Eye gaze may thus be a special cue in orienting attention and modulating subsequent early visual processing.

It should be noted, however, that the amplification and acceleration of sensory processes following congruent eye gaze cues were found with a cue in motion: the face first gazed at the observer for half a second and then the eyes moved either to the left or to the right, shortly before the onset of the lateralized target (Schuller and Rossion, 2001). Although behavioural studies have shown that both dynamic and static eye cues give rise to shorter reaction times to validly cued targets (Friesen and Kingstone, 1998; Driver et al., 1999; Hietanen, 1999; Langton and Bruce, 1999; Vuilleumier, 2002), it is yet unclear whether the early visual potential effects mentioned earlier can also be observed with static cues. In fact, a possible role of motion in the gaze effect is suggested by developmental studies, showing that 3–5-month-old infants orient their attention following gaze direction (Hood et al., 1998; Farroni et al., 2000, 2003). This orienting appears to depend upon the direction of the visual motion cue and not upon the specific gaze direction: infants make faster saccades to congruently cued targets only when the eyes are moving to the side; when the eyes are static, no attentional advantage is noticed (see experiment 3 in Farroni et al., 2000). In a follow-up study, Farroni et al. (2003) showed that the direction of eye motion was only effective as a cue when preceded by a direct gaze. The importance of eye motion is also indirectly indicated by ERP studies on gaze direction discrimination (Puce et al., 2000; Taylor et al., 2001) measuring the N1 in response to faces (the N170; Bentin et al., 1996).

In the present study, we investigated whether a static eye direction elicits similar attentional effects on the amplitude and latency of the early visual responses evoked by a target, as does a dynamic eye cue (Schuller and Rossion, 2001).

The second point addressed by the present study is whether the processing of visual stimuli is facilitated by attention cued by eye-gaze, or if it is rather the processing of the unattended stimuli that is suppressed. In experimental studies of spatial attention, this question is usually investigated by adding a neutral cueing condition in the design (Posner, 1980). During neutral trials, attention is presumably unfocused or broadly focused and thus provides a baseline condition that allows to distinguish between behavioural cost effects (linked to neuronal suppression mechanisms) and benefit effects (facilitation mechanisms) of attention. For instance, Friesen and Kingstone (1998, 2003b) used a schematic face staring straight ahead as a neutral condition and showed that validly cued targets were detected faster than targets of either neutral or invalid trials (attentional benefit), with no difference between the latter two (no cost). Whether these

facilitation effects are reflected in the early sensory ERP responses will thus be investigated here using a neutral condition, where the central face was staring at the observer.

2. Methods

2.1. Subjects

Twelve paid volunteers (7 males, two left handed, aged 21–27 years) participated in the study. All of them had normal or corrected to normal vision.

2.2. Stimuli and procedure

Subjects were seated in a comfortable chair in a dimly lit, electrically shielded room, at a distance of 80 cm from a monitor screen, their head restrained by a chin rest. Stimuli were one picture of a full front female face with the eyes fixating the viewer, and two pictures of the same face with eye gaze averted, towards the left and right visual field (see Fig. 1). The 3 face photographs subtended a visual angle of 7.15° vertically and 3.9° horizontally, and were presented on a white background. A simple black cross (0.5/0.5°) was used as a target.

A trial was made of the following events: a face gazing at the viewer, or looking left or right, presented for 500 ms; followed by a lateralized cross (target), appearing randomly in half of the trials in the right visual field (RVF), and in the other half in the left visual field (LVF), at a distance of 6.8° of visual angle from the centre of the screen (Fig. 1). The central face and the target remained on the screen until the subject's response. The next trial was presented after a 500 ms delay.

The experiment consisted of 4 blocks randomly composed of 90 congruent, 90 incongruent and 70 neutral trials. Twelve catch trials, where no target followed the cue and no answer was required, were also presented to maintain the attention of the subjects during the experiment, and to prevent anticipations. Throughout the experiment, subjects were instructed to maintain fixation at the central face. Subjects were required to press a left button of the response box when the target was shown in the LVF and a right button when the target was presented in the RVF, using their dominant hand. They were asked to be as accurate and as fast as possible. Twenty trials were run before starting the experiment to familiarize the subjects with the task. Subjects knew that the direction of eye gaze was not predictive of the location of the following target.

2.3. ERP recordings and data analysis

Recordings were made using tin electrodes in a 64 channel modified quick-cap (Neuromedical Supplies Inc.), with 6 additional low occipito-temporal electrodes

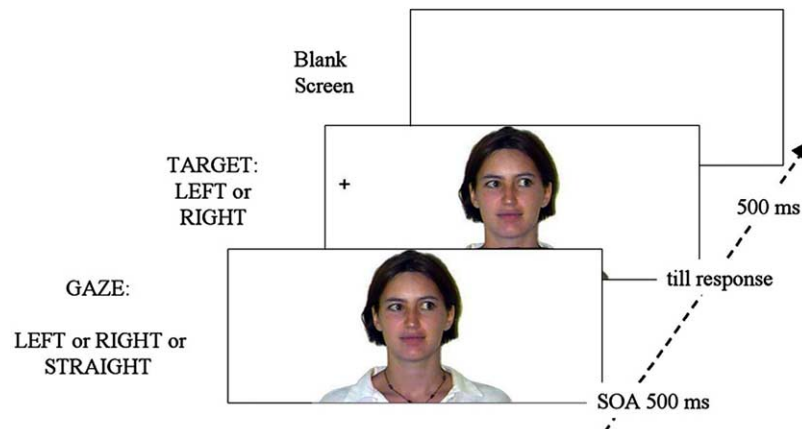


Fig. 1. Stimulus sequence used in the present experiment; here an incongruent trial (target location opposite to the gaze direction) is illustrated.

(TP9/TP10, P9/P10, PO9/PO10). Horizontal EOG recording electrodes were positioned at the outer canthi of both eyes and vertical EOG recording electrodes were placed above and below the left eye. The reference electrode was positioned on the tip of the nose. EEG was amplified with a gain of 30 K and bandpass filtered between 0.01 and 100 Hz. Electrode impedances were kept below 5 k Ω . EEG and EOG were sampled at a digitization rate of 500 Hz. The EEG was filtered off-line between 2 Hz (high-pass) and 20 Hz (low-pass) to get rid of drifts and slow waves (e.g. CNV) related to subject's anticipation (Vogel and Luck, 2000) and to facilitate automatic peak detection on ERP waveforms respectively. Then EEG and EOG artefacts were removed using a $[-40; +40 \mu\text{V}]$ deviation over 200 ms intervals on all electrodes. In case of too many blink artefacts (in 5 subjects) they were corrected by a subtraction of VEOG propagation factors, based on PCA-transformed EOG components (Nowagk and Pfeifer, 1996). Averages were generated for each subject and each of the conditions in epochs of -200 to 800 ms. Correct trials only were considered. The number of sweeps averaged (after artefact rejection and removal of incorrect trials) was equalized within each subject for the 3 conditions, by a random selection procedure (32 trials on average for each visual field).

2.4. Data analysis

Following visual inspection of scalp topography, peak latency of the visual components P1 and N1 was extracted automatically for each subject and condition on electrode pair P3/P4, where these components were most prominent on the scalp distribution of grand-averaged data and could be extracted accurately for all averages. Amplitude values were measured on 4 pairs of electrodes (P3/4, P5/6, PO3/PO4, PO5/PO6), as the mean of a 20 ms window centred on the grand-average peak latencies of the P1 and N1 for each channel and each condition separately (see Table 1). This procedure was

more accurate and sensitive than using a fixed window for all conditions, given the significant differences of peak latencies between the experimental conditions (congruency), hemispheres and lateralization of the target (LVF/RVF). To take into account P1 differences in assessing the N1 effects, analyses were also computed on peak-to-peak differences between N1 and P1 amplitude and latency values. Repeated-measures analyses of variance (ANOVAs) and planned mean comparisons were performed on RT and ERP measurements. Greenhouse-Geisser correction was used to correct P values for factors containing more than two levels. The report of the results focuses on the description of the attentional modulations. Given that electrode position and hemispheric ERP differences due to the lateral field stimulation have been well described in the literature (e.g. Martinez et al., 1999) and in our previous study (Schuller and Rossion, 2001), they will be only briefly reported here, without an explicit description of all interactions between these factors.

3. Results

3.1. Behaviour

Accuracy was almost at ceiling for all conditions (less than 3% of errors). The one-way ANOVA on RTs showed a significant main effect of congruency ($F(1.3, 14.7) = 8.025$; $P < 0.009$). RTs were faster for targets detected at congruent locations (306 ms) compared to targets appearing at incongruent locations (325 ms, $P < 0.005$), and to neutral trials (321 ms, $P < 0.03$) (Fig. 2). There was no difference between incongruent and neutral trials.

3.2. Event-related potentials

As expected, lateralized targets elicited a sequence of clear occipito-parietal P1 (peaking around 125 ms) and N1

Table 1

Grand-average latency values and peak amplitude for parietal and occipital-temporal electrodes corresponding to the P1 and the N1 component

		Left hemisphere				Right hemisphere			
		P3	P5	PO3	PO5	P4	P6	PO4	PO6
P1									
LVF congruent	Latency	128	128	128	128	122	122	126	124
	Amplitude	2.59	2.51	3.18	3.10	2.83	3.03	2.56	2.63
LVF incongruent	Latency	132	132	132	132	128	128	130	130
	Amplitude	2.22	2.09	2.64	2.63	2.18	2.44	2.19	2.14
LVF neutral	Latency	134	134	132	132	128	128	132	130
	Amplitude	2.55	2.48	3.10	3.06	2.47	2.80	2.26	2.23
RVF congruent	Latency	114	116	118	118	126	126	126	124
	Amplitude	1.65	1.63	1.82	1.87	2.32	2.76	1.85	1.99
RVF incongruent	Latency	114	114	118	116	126	126	120	120
	Amplitude	2.13	2.10	2.23	2.35	1.79	2.04	1.49	1.56
RVF neutral	Latency	114	116	118	118	124	124	122	122
	Amplitude	1.84	1.71	1.99	2.05	2.03	2.37	1.63	1.73
N1									
LVF congruent	Latency	178	178	178	180	174	174	178	178
	Amplitude	-2.86	-2.72	-3.69	-3.41	-5.73	-5.25	-4.26	-4.36
LVF incongruent	Latency	190	184	186	188	176	176	182	182
	Amplitude	-2.20	-1.95	-2.71	-2.51	-4.37	-4.00	-3.30	-3.27
LVF neutral	Latency	180	180	180	180	176	176	180	180
	Amplitude	-2.72	-2.56	-3.62	-3.37	-4.88	-4.53	-3.76	-3.73
RVF congruent	Latency	170	170	170	170	174	174	172	172
	Amplitude	-3.54	-3.32	-3.36	-3.46	-2.84	-2.56	-2.61	-2.68
RVF incongruent	Latency	172	170	174	174	188	186	182	186
	Amplitude	-3.12	-2.99	-3.06	-3.28	-1.95	-1.65	-1.74	-1.69
RVF neutral	Latency	174	172	176	176	184	184	182	180
	Amplitude	-2.78	-2.63	-2.91	-3.02	-1.50	-1.27	-1.44	-1.42

(around 180 ms) components (see Fig. 3 and Table 1). These two components were lateralized with respect to the side of the stimulation (maximal and earlier in response to contralateral stimuli on grand-averaged data) and appeared to peak earlier and to be larger in response to targets appearing at an eye-gaze cued location (Table 1 and Fig. 3).

3.2.1. P1

There was a significant main effect of congruency on the P1 latency ($F(1.3, 14.5) = 5.325$; $P < 0.03$). When the target location was congruent with the eye gaze direction, the P1 peaked significantly earlier (congruent: 124 ms) than when evoked by a target cued by an opposite gaze direction (incongruent: 129 ms; $P < 0.05$), or when it was not cued at all (neutral: 129 ms; benefit: $P < 0.01$). There was no difference between the latter two conditions (Fig. 3 and Table 1). As expected, the visual field of stimulation interacted significantly with the factor hemisphere ($F(1, 11) = 22.839$; $P < 0.001$), the P1 peaking earlier in the contralateral compared to the ipsilateral hemisphere (RVF: $P < 0.05$; LVF: $P < 0.005$).

There was no significant main effect of congruency on the P1 amplitude. However, there was a significant interaction between congruency and hemisphere ($F(1.9, 21.3) = 4.914$; $P < 0.05$). In the right hemisphere,

there was a significant larger P1 for the congruent condition compared to the incongruent ($P < 0.0001$) and neutral conditions ($P < 0.0001$) (Fig. 3). The P1 amplitude was identical for incongruent and neutral trials. In the left hemisphere, no significant differences were found (all

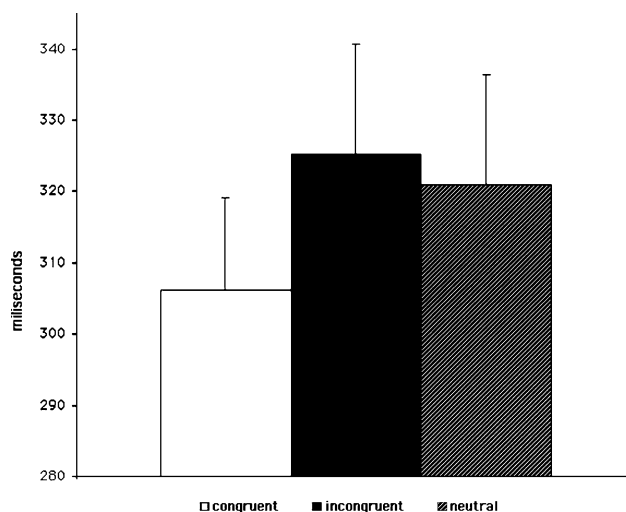


Fig. 2. Reaction times (in ms) and standard deviation plotted for the congruent, incongruent and neutral conditions.

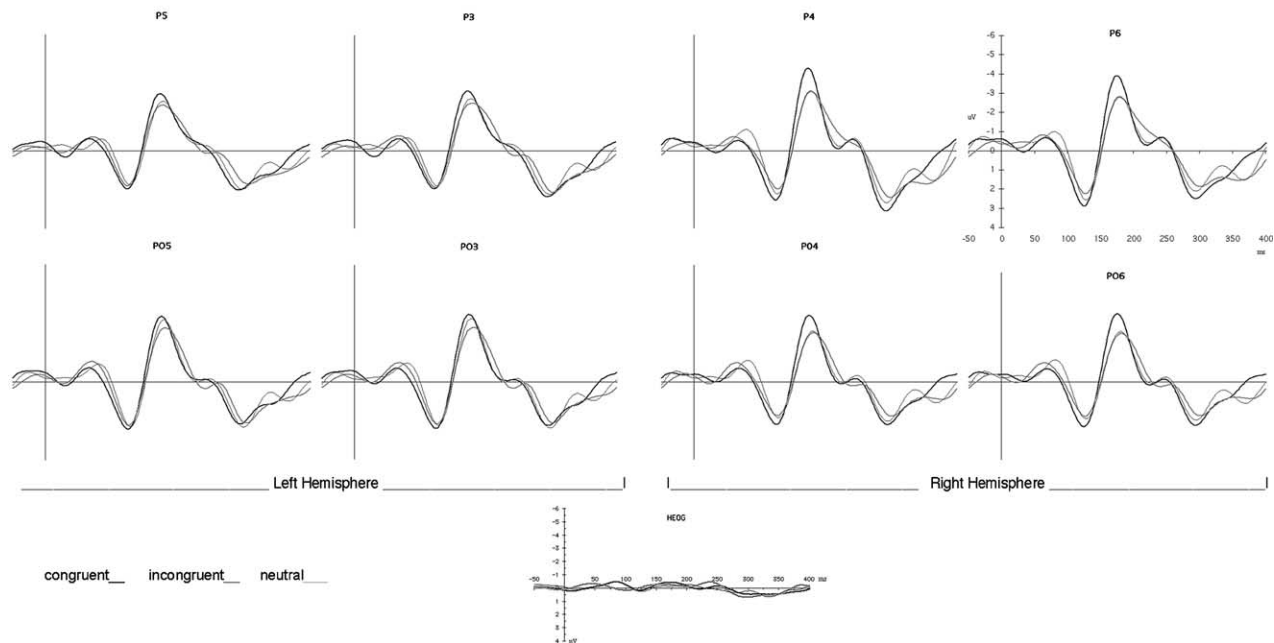


Fig. 3. Grand-averaged ERP waveforms for the 3 cueing conditions shown on electrodes covering the temporal-occipital scalp of the left and right hemisphere. Below, grand-average horizontal electrooculogram (HEOG) displayed for the same 3 cueing conditions. LVF and RVF ERPs are plotted together. ERPs plotted in black represent congruent trials, grey lines denote incongruent trials, and thin grey lines correspond to neutral trials.

$P_s > 0.2$). Besides these main effects of attentional facilitation in the right hemisphere, no other congruency effects were noticed. A significant interaction was observed between the factors hemisphere and electrode ($F(1.7, 18.6) = 5.209$; $P < 0.005$).

3.2.2. N1

There was a main effect of congruency ($F(1.8, 19.4) = 4.629$; $P < 0.03$) on the N1 latency, the N1 evoked by a congruently cued target peaking 4 ms earlier than during the incongruent and neutral conditions ($P < 0.02$ for the two effects; no differences between neutral and incongruent; see Table 1 and Fig. 3). However, when accounting for P1 latencies (ANOVA on peak latency differences between P1 and N1), there were no reliable effects of congruency on the N1 peak latency.

There was a non-significant trend of congruency for the N1 amplitude ($F(1.7, 18.5) = 3.241$; $P = 0.069$). The interaction between congruency and hemisphere showed a similar trend ($F(1.8, 20.3) = 3.125$; $P = 0.069$). Planned comparisons indicated that congruent trials gave rise to a significantly larger N1 compared to incongruent trials, and the magnitude of this effect was dependent on the hemisphere (LH: $P < 0.02$; RH: $P < 0.0001$). The N1 amplitude measured over the right hemisphere was significantly amplified for congruent trials compared to neutral trials ($P < 0.0001$), but there were no such facilitation effects in the left hemisphere. There were no suppression effects, neither in the left nor in the right hemisphere.

There was no main effect of congruency on the peak-to-peak N1 amplitude values. However, there was a significant interaction between congruency and hemisphere ($F(1.9, 20.4) = 5.967$; $P < 0.01$): in both hemispheres, the N1 responses to congruent trials were significantly larger than those to incongruent trials, but this difference was larger in the right hemisphere (LH $P < 0.05$; RH: $P < 0.0001$, see Table 1 and Fig. 3). Furthermore, a facilitation effect was noticed over the right but not over the left hemisphere (congruent vs. neutral: RH: $P < 0.0001$). No reliable differences were found between incongruent and neutral trials, neither in the right nor in the left hemisphere. Additional significant interactions were found between target location and hemisphere ($F(1, 11) = 4.94$; $P < 0.05$) and between electrode site and hemisphere ($F(1.4, 15.2) = 7.648$; $P < 0.01$). There was also a triple interaction between electrode site, hemisphere and target location ($F(1.5, 16.0) = 4.43$; $P < 0.05$).

4. Discussion

The present results extend prior work on attentional orienting by eye gaze direction, showing that (1) static, and not only dynamic, eye gaze cues can modulate subsequent early visual processing, and that (2) these attentional orienting effects reflect processing facilitation of congruent/attended stimuli.

4.1. Behavioural effects of eye gaze cueing

Behavioural findings confirm the results of previous studies reporting that eye gaze perception produces reflexive¹ orienting (Friesen and Kingstone, 1998, 2003a; Driver et al., 1999; Hietanen, 1999; Schuller and Rossion, 2001; Vuilleumier, 2002). In the present study too, targets appearing at the gazed-at locations were detected faster than targets appearing at the opposite locations, even though the subjects were aware of the nonpredictive value of the eye gaze direction, and maintained central fixation (see Fig. 3). In addition, the present congruency effects obtained with the static eye gaze stimuli were roughly of the same order of magnitude than those we observed with the same stimuli in motion (Schuller and Rossion, 2001), suggesting that, contrary to what is found in infants (Farroni et al., 2000, 2003), adults' gaze orienting effects do not appear to depend on the perception of apparent eye motion. In addition, targets presented during neutral trials were detected with the same speed than targets in the incongruent trials, confirming that attentional orientation following eye gaze is mainly expressed as a benefit effect (Friesen and Kingstone, 1998, 2003b; Hietanen, 1999², 2002), i.e. speeding up the response to the gazed-at target without slowing down the detection of the incongruent target.

4.2. ERPs

ERPs recorded during processing of the target following static eye gaze cueing replicated previous findings (Schuller and Rossion, 2001) and showed a speeding up and an amplification of early visual processes, as reflected by visual components P1 and N1, in the absence of visual motion in the eye gaze cues. Amplitude enhancement of visual components P1 and N1 has been reported in numerous spatial attention studies and is thought to reflect an attentional sensory gain control mechanism, modulating the information flow differentially between attended and unattended parts of the visual field (for reviews see Hillyard et al., 1998; Luck et al., 2000). The sources of the P1 component have been located in ventral-lateral cortex/posterior fusiform gyrus for stimuli presented in upper visual field (Gomez Gonzales et al., 1994; Heinze et al., 1994; Mangun et al., 2001), and in dorsal extrastriate cortex when the P1 was evoked by lower visual field stimulation (Woldorff et al., 1997). Recent evidence has supported

this dorsal/ventral dissociation for the P1 attentional effects, suggesting that the early (80–100 ms) enhancement of the P1 due to spatial attention can be accounted for by dorsal sources, in the lateral mid-occipital cortex for both upper and lower field stimuli, whereas the latter phase of the P1 (100–130 ms) originates from the ventral occipital cortex (Martinez et al., 1999, 2001; Di Russo et al., 2002, 2003). The enhanced N1 component was estimated to arise from multiple generators in the occipito-parietal and occipito-temporal cortex, partly overlapping with the P1 generators (Gomez Gonzales et al., 1994; Clark et al., 1995; Clark and Hillyard, 1996; Di Russo et al., 2003).

In the present study, in addition to the amplitude enhancement, the peak latency of the P1 to congruent trials was shorter than the P1 latency for incongruently cued targets, again replicating our previous observations (Schuller and Rossion, 2001). This replication of the latency effect is particularly significant, since it pinpoints the power of the spatial orienting triggered by eye gaze as a dynamic or static cue, modulating even the onset of visual processing as early as ~100 ms. Using dynamic gaze cueing, latency effects were also observed on the N1 component (Schuller and Rossion, 2001). Here, there was also a difference in the N1 latency between congruent and incongruent conditions (Fig. 3 and Table 1), but when the peak latency of the P1 was taken into account, this N1 latency difference disappeared. To our knowledge, only a few spatial attention studies observed latency differences of VEPs (Wright et al., 1995; Di Russo and Spinelli, 1999; Di Russo et al., 2001). Whereas Wright et al. (1995) did not find reliable latency modulations on processing stages before 300 ms post-stimulus, Di Russo and Spinelli (1999) and Di Russo et al. (2001) reported attentional latency effects on transient and steady-state VEP components peaking as early as 60 ms after stimulus onset. The latency modulations could also result from an enhanced efficiency in sensory processing, but the exact neural mechanisms underlying these effects are currently unclear (Schneider and Bavelier, 2003).

Similarly to amplitude modulations, the latency effects observed at the level of the P1 appear to reflect facilitation in processing congruent targets rather than an inhibition in processing incongruent stimuli. Previous spatial attention ERP studies using a neutral cue were based on different paradigms and task demands, and obtained diverging results. For instance, Luck et al. (1994), using a symbolic trial-by-trial cueing paradigm to measure the effects of spatial attention on a near threshold luminance detection task, found a suppression effect on the P1, but a facilitation effect on the N1 amplitude. The authors claimed that the P1 attentional effect represents the inhibition of interfering information coming from the unattended location, whereas the N1 attention effect was interpreted as reflecting a relatively pure enhancement of attended-location stimuli rather than a combination of attended-location enhancement and ignored-location suppression (Luck et al., 1994). On the other hand, facilitation effects on the P1 were reported

¹ The term 'reflexive' orienting is used, as in previous behavioural studies using this eye gaze paradigm (e.g. Langton et al., 2000; Friesen and Kingstone, 1998, 2003a,b), to refer to an orienting which has the properties of exogenous cueing mechanisms: it is rapid and it occurs even when the cue is not predictive. However, these reflexive gaze shifts do not share all properties of the classical exogenous cueing, which was originally called reflexive. For instance it occurs out of a centrally presented cue, it is long lasting and it does not show any inhibition of return (see Friesen and Kingstone, 2003a).

² Although both benefit and cost effects were observed in that study.

in a sustained attention paradigm (Proverbio and Mangun, 1994; Mangun and Buck, 1998) and suppression effects on the N1 in a trial-by-trial cueing design (Eimer, 1996). Based on these different results, it was suggested that the P1 and N1 attentional modulations reflect distinct mechanisms of attention. However, in the present study, independent facilitation effects on both P1 and N1 components were observed, in agreement with the behavioural observations.

Evidence from face and eye gaze processing studies, together with results from attentional studies, support the right hemispheric dominance found in the present study. A left visual field advantage has recently been described for perception of eye direction (Ricciardelli et al., 2002), in agreement with the well-known right hemispheric dominance for face processing, shown by neuropsychological investigations (e.g. Farah, 1990), neuroimaging studies (e.g. Sergent and Signoret, 1992; Rossion et al., 2000) and behavioural evidence from divided visual field studies (Hillger and Koenig, 1991). In addition, several attentional studies have shown that the right hemisphere is able to mediate attention bilaterally to the visual space, whereas the left hemisphere is able to mediate attention to the contralateral side of the visual space only (Mesulam, 1981, 1999; Proverbio et al., 1994). Recent evidence coming from transcranial magnetic stimulation (TMS) emphasizes these hemispheric asymmetries in spatial attention (Grosbras and Paus, 2002).

In conclusion, ERP evidence supports the view that spatial attention triggered by static eye gaze direction produces response facilitations – predominantly lateralized to the right hemisphere – from the early sensory stages of visual processing.

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