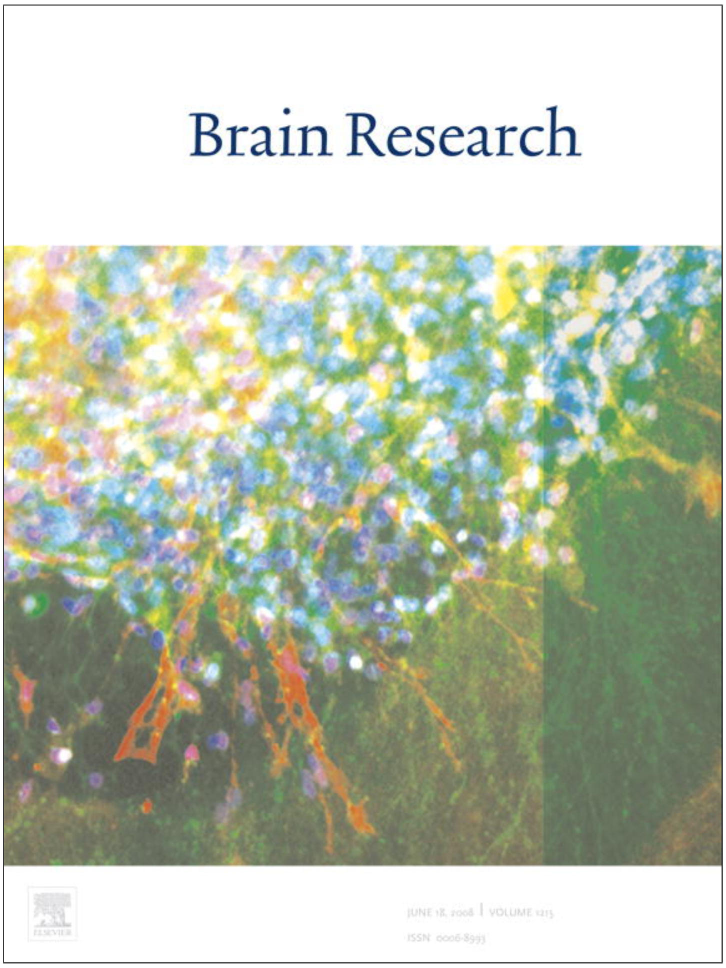
Brain Research
ELSEVIER
JUNE 18, 2008 | VOLUME 1215
ISSN 0006-8993

BRAIN RESEARCH 1215 (2008) 123–136

available at www.sciencedirect.com

ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

Visuospatial attention shifts by gaze and arrow cues: An ERP study

Jari K. Hietanen[a,*], Jukka M. Leppänen[a], Lauri Nummenmaa[b], Piia Astikainen[c]

[a]Human Information Processing Laboratory, Department of Psychology, University of Tampere, Finland
[b]MRC Cognition and Brain Sciences Unit, Cambridge, UK
[c]Department of Psychology, University of Jyväskylä, Finland

ARTICLE INFO

Article history:
Accepted 9 March 2008
Available online 13 April 2008

Keywords:
Gaze
Attention
Orienting
Human
Event-related potential

ABSTRACT

Orienting of visual attention can be automatically triggered not only by illumination changes occurring in the visual periphery but also by centrally presented gaze and arrow cues. We investigated whether the automatic shifts of visuospatial attention triggered by centrally displayed gaze and arrow cues rely on the same neural systems. To this end we measured event-related potentials (ERPs) time-locked to the cue and target onsets while the participants ($n = 17$) performed a spatial cuing task. In the task, the participants detected and responded to laterally presented targets preceded by centrally presented, non-predictive, gaze or arrow cues. Manual reaction times and target-triggered ERP data showed that both gaze and arrow cues automatically oriented attention and facilitated subsequent processing of target stimuli. However, the cue-triggered electrophysiological data indicated that the ERPs elicited by the gaze and arrow cues were different at lateral parietal and fronto-central electrode sites. Most notably, for the arrows, we found a typical early attention direction negativity (EDAN) effect occurring 220–260 ms after the cue onset. The ERPs were shifted in the negative direction when the arrows pointed to a direction which was contralateral to the recorded hemisphere as compared to arrows with ipsilateral direction. This effect was not observed for the gaze stimuli. These results provide further support for earlier behavioral and neuroimaging studies indicating that automatic orienting of attention by arrow cues and gaze cues are based on different neural mechanisms.

1. Introduction

Several recent studies have suggested that automatic orienting of visuospatial attention can be triggered not only by peripherally displayed illumination changes (Posner, 1980), but also by centrally presented social gaze cues (e.g., Driver et al., 1999; Friesen and Kingstone, 1998; Hietanen, 1999) and symbolic arrow cues (Hommel et al., 2001, Experiment 3a; Ristic et al., 2002; Tipples, 2002). Both gaze-cued and arrow-cued orienting seems to fulfill two important criteria of automatic shifts of attention. First, the cuing effect – shorter reaction times (RT) to laterally presented targets shown after valid than invalid spatial cues – is observed even when the cues do not predict the location of the upcoming targets. Second, the cuing effect is observed even when the time interval between cue and target onset is short (e.g., stimulus-onset-asynchrony, SOA of 100 ms).

Dual-process theories of attention (Barrett et al., 2004; Corbetta and Shulman, 2002; Egeth and Yantis, 1997) distinguish

---

[*] *Corresponding author*. Human Information Processing Laboratory, Department of Psychology, 33014 University of Tampere, Finland. Fax: +358 3 3551 7345.

E-mail address: jari.hietanen@uta.fi (J.K. Hietanen).

0006-8993/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2008.03.091

between goal-driven (voluntary, controlled) and stimulus-driven (reflexive, automatic) mechanisms of attention orienting. Before the first experiment showing reflexive gaze cuing (Friesen and Kingstone, 1998), the prevailing view was that only peripheral but not central cues prompt reflexive shifts of attention (Jonides, 1981; Posner, 1980). Thus, the finding of gaze cues triggering automatic attention orienting was interpreted to suggest that another individual's gaze is a special, socially and biologically relevant stimulus capable of engaging the reflexive attention orienting mechanism. However, the special nature of gaze-cued orienting was challenged by findings of biologically non-relevant symbolic cues, such as arrows, also triggering automatic shifting of attention. What evidence, then, do we have to support the notion that attention orienting by an averted gaze is mediated by specialized neural mechanisms?

One line of evidence comes from studies indicating that gaze cuing really relies on the neural mechanisms sensitive to the perception eyes, eye-movements, and gaze direction. These networks are found in the area of the superior temporal sulcus, STS (e.g., Akiyama et al., 2006a; Allison et al., 2000; Calder et al., 2007; Hoffman and Haxby, 2000; Pelphrey et al., 2004; Perrett et al., 1992; Taylor et al., 2001a; Wicker et al., 1998). Kingstone et al. (2004) used functional magnetic resonance imaging (fMRI) to investigate brain activation during an attention orienting task in which the attention-directing cue was an ambiguous figure. The ambiguous figure was introduced to the participants either as a face with averted eyes or as a car with eccentric wheels. The behavioral cuing effect was observed in both situations. However, the STS activity was increased when the cue was perceived as a face with averted eyes as compared to when it was perceived as a car. Hooker et al. (2003) have also shown that STS is more strongly activated when participants judge whether the gaze shifts to one of the pre-determined target locations than when they perform a similar task with arrows. The role of the STS region for gaze-cued orienting is also implicated in a case study with a patient M.J. having a lesion in the right superior temporal gyrus (STG) and showing intact cuing effect by arrows but not by gaze cues (Akiyama et al., 2006b).

Together these results from imaging and lesion studies provide strong evidence that visual attention orienting by gaze cues truly relies on visual information from the face analyzed by face/gaze-specific and not by some kind of a general-purpose mechanism analyzing all types of visual directional information. However, it should be noted that although these results tend to indicate that the visual analysis of gaze and arrow cues is based on different neural mechanisms, they tell us little about whether there are also differences in the neuro-cognitive mechanisms following the visual analysis of the cues, i.e., mechanisms subserving visual attention orienting. For example, Akiyama et al. (2006a) have actually shown that the STG-lesion patient M.J. is inaccurate in gaze direction judgments. Thus, it is not surprising that he does not demonstrate the gaze cuing effect.

Vuilleumier (2002) tested three patients with right parietal damage (and left neglect) in non-predictive cuing tasks in which schematic gaze (Experiments 4 and 5) and arrow (Experiment 6) stimuli served as cues. The results showed that, in these patients, the non-predictive gaze cues triggered attentional shifts whereas the non-predictive arrow cues failed to do so. As the lesions involved the parietal area networks known to be involved in voluntary control of visuospatial attention (Corbetta and Shulman, 2002), it is likely that the failing of arrows but not gaze cues in reflexively shifting attention in these patients reflected the differential dependence of these cues on parietal attention orienting systems. More specifically, the results suggest that the "reflexive" orienting by arrow cues might actually be contingent on the rapid engagement of the neural system for voluntary attention orienting (see Corbetta and Shulman, 2002). Friesen et al. (2004) provided evidence from a behavioral reaction time study with normal subjects suggesting that gaze and arrow cues trigger qualitatively different forms of orienting. They used a so-called counter-predictive cuing paradigm and showed that despite of a strong (induced) subjective bias to expect the target to appear at the opposite to gazed-at location, the gaze cues, nevertheless, resulted in attention shifts to the gazed-at locations. Similar results were reported earlier by Driver et al. (1999, Experiment 3). Importantly, when counter-predictive cuing was tested with arrows, participants' attention did not shift to the cued-at locations. Gaze cuing was, thus, suggested to be less susceptible to top-down influences. In another study, Langdon and Smith (2005) demonstrated that non-predictive arrow and gaze cues resulted in different patterns of RT benefits and costs. When compared to a neutral cue, valid arrow cues elicited shortened reaction times (facilitation) but invalid arrows did not lead to lengthened RTs (inhibition). Instead, valid and invalid gaze cues resulted in facilitation and inhibition, respectively. The authors concluded that gaze cues are capable of triggering true reflexive attentional orienting characterized by costs and benefits, whereas the RT advantages resulting from valid arrow cues are more likely due to automatic, non-attentional priming.

More recently, Hietanen et al. (2006) directly investigated whether the shifts of attention triggered by gaze cues and arrow cues rely on the same neural systems by measuring hemodynamic responses resulting from gaze-cued and arrow-cued orienting with fMRI. Behavioral data showed that, for both cue types, reaction times were shorter on valid than invalid trials, but the imaging data indicated that gaze-cued and arrow-cued attention orienting activated different cortical networks. For gaze-cued orienting, three relatively small foci of activation in the left inferior occipital gyrus and right medial and inferior occipital gyri were revealed. For arrow-cued orienting, a much more extensive network was activated. There were large bilateral post-central activations in areas including the medial/inferior occipital gyri and medial temporal gyri, and in the left intraparietal area. Interestingly, arrow cuing also activated the right frontal eye field and supplementary eye field. The results were interpreted to suggest that attention orienting by gaze cues and attention orienting by arrow cues are not supported by the same cortical network and that attention orienting by symbolic arrow cues relies on mechanisms associated with voluntary shifts of attention.

In the present study, we continued studying the neural substrates of attention orienting by non-predictive gaze and arrow cues by measuring event-related potentials (ERP) evoked by these two cue types. In the previous fMRI study (Hietanen et al., 2006), a blocked-design was used and it was not possible to investigate the time-course of the hemodynamic responses related to attention orienting. By using the ERP technique we obtained data with high temporal resolution to complement the previous neuroimaging results. There is a good deal of previous research that has measured ERPs to centrally presented arrow cues during a spatial attention orienting task. It has been shown that three arrow-triggered ERPs are shifted in the negative or positive direction for cues pointing to the direction which is contralateral to the recorded hemisphere as compared to cues with ipsilateral direction. These are elicited by non-predictive arrow cues, i.e. arrows which do not indicate the side of an upcoming target (Harter et al., 1989; Hopf and Mangun, 2000), as well as by predictive arrow cues (Nobre et al., 2000; Talsma et al., 2005; Van der Lubbe et al., 2006; Yamaguchi et al., 1994).

Irrespective of the predictive nature of the cue, the first direction-related component is a posterior (occipital–parietal) negativity between 200 and 400 ms after cue onset (Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Talsma et al., 2005, Van der Lubbe et al., 2006; Yamaguchi et al., 1994). This negativity has been labeled the "early directing attention negativity" (EDAN, Harter et al., 1989) and it has been proposed to reflect the re-directing of spatial attention (Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994).

The second component is an anterior negativity at around 300–500 ms after the cue onset (Hopf and Mangun, 2000; Nobre et al., 2000; Talsma et al., 2005; Van der Lubbe et al., 2006). This component, the anterior directing attention negativity (ADAN), has been suggested to reflect activity of the frontal attention-controlling areas. The third component is a posterior positivity evoked after about 500–700 ms (Harter et al., 1989; Hopf and Mangun, 2000; Van der Lubbe et al., 2006). This component has been referred to as the late attention-directing attention positivity (LDAP), and it has been suggested to reflect the influence of attention on processing of visual information along the ventral stream (Hopf and Mangun, 2000).

Besides ERPs to direction-specific cue reviewed above, previous studies have also investigated ERP responses to orienting of attention independent of the cue direction. This has been carried out by comparing ERPs to directional (collapsed across left and right) and non-directional (neutral) cues. Talsma et al. (2005) used predictive arrow cues and showed that between 160 and 400 ms after the cue onset, fronto-central ERPs to directional cues were shifted in the positive direction relative to ERPs to non-directional cues. Wright et al. (1995) also employed predictive arrow cues and reported enhanced P3 wave to directional cues at the posterior channels (Pz and Oz). Talsma et al. (2005) suggested that the fronto-central positivity to directional cues reflects the engagement of mechanisms directing attention to a spatial location.

Even though the current study was focused on the ERPs evoked by the arrow and gaze cues, we also wanted to measure and analyze ERPs evoked by the targets. Previous research has shown that that the early visual P1 and N1 components are enhanced to targets preceded by valid arrow cues (Eimer, 1997; Hopf and Mangun, 2000; Luck et al., 1994; Mangun and Hillyard, 1991; Nobre et al., 2000; Talsma et al., 2005) and valid gaze cues (Schuller and Rossion, 2001, 2004, 2005) as compared to respective invalid cues. These results have been interpreted to show that the shifts of attention enhance the processing of visual information at the cued location in the early visual areas. Schuller and Rossion (2001, 2004, 2005) have also reported shorter latencies of P1 and N1 components for valid than invalid gaze cue trials. By measuring the target-triggered ERPs, in the present study, we were able to investigate if the attentional effects on the early visual processing of the targets differ depending on whether the attention shifts are triggered by the arrow or gaze cues.

We employed ERP measurements to compare attention orienting related neural activity evoked by arrow cues ("traffic signs") and simple schematic gaze cues (faces). The participants were performing a standard cuing task in which a single non-predictive (i.e., 50% valid) arrow or gaze cue was presented on each trial. The cues were either directional, i.e., an arrow/gaze cue directed either to the left or right, or non-directional, i.e., a segment of a line or a direct gaze. The targets were subsequently presented to the left or right, independently of the cue direction. The stimuli (see Fig. 1) were the same as in the previous neuroimaging study (Hietanen et al., 2006). Regarding the ERP responses to directional arrow and gaze cues, we targeted our main interest on EDAN and ADAN effects on ERP amplitude waveforms. Because we used an SOA of 500 ms, only these two attention-directing related brain responses were of interest in the present study. We also investigated the brain responses to directional (i.e., averaged ERPs elicited by left and right cues) vs. non-directional (neutral) cues. Considering that a previous neuroimaging study showed a smaller network of activated posterior areas for gaze-cued than arrow-cued orienting and that arrow cuing, but not gaze cuing, also activated frontal areas (Hietanen et al., 2006), it was expected that the posterior EDAN evoked by arrow cues would be larger and differently distributed than that evoked by gaze cues and that only the arrow cues would elicit the anterior ADAN. Likewise, regarding the responses to directional vs. non-directional cues, it was anticipated that the fronto-central positivity to directional cues would be more pronounced for the arrow than gaze cues. Finally, we expected that the early visual ERPs to targets following the arrow and gaze cues would be larger and their peak latency shorter when preceded by valid than invalid cues.

2. Results

2.1. Behavioral data

The reaction times (from the presentation of the reaction signal to the press of the response key) were analyzed as follows: First,

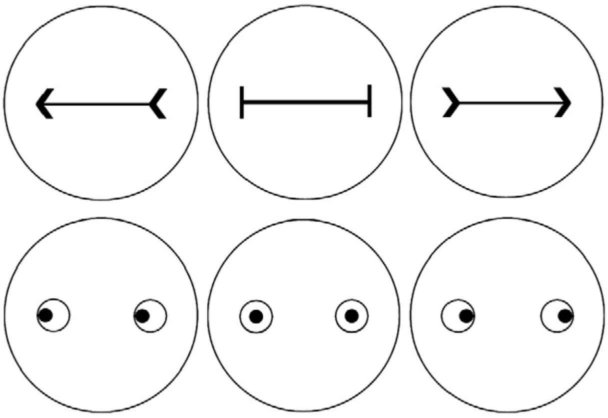

Fig. 1 – Arrow and gaze cue stimuli used in the experiment.

responses with reaction times shorter than 100 ms and longer than 1000 ms were excluded from the data analysis. Next, responses with reaction times 2SD:s above and below each subject's mean were filtered. Based on these criteria, 4.2% of the trials were discarded. Finally, the mean reaction time for both cue types in each stimulus condition was calculated for each participant. On average, participants made 10.0% catch trial errors (pressed the response button when there was no reaction signal).

In order to analyze whether the gaze and arrow cues shifted the participants' attention, RTs in valid, neutral, and invalid conditions cued by gaze and arrow cues (see Fig. 2) were compared by subjecting them to a 3 (Cue validity: valid / neutral/invalid) × 2 (Cue type: arrow/gaze) repeated measures ANOVA [the degrees of freedom were adjusted by Greenhouse–Geisser epsilon (ε) when the sphericity assumption was violated]. The analysis yielded significant main effects for Cue validity [$F(2,32)=22.1$, $p<.001$, $\varepsilon=.76$, $\eta^2_p=.58$] and Cue type [$F(1,16)=19.7$, $p<.001$, $\eta^2_p=.55$]. The Cue validity × Cue type interaction was not significant [$F(2,32)=1.5$, $p>.2$]. Although the interaction was not significant, it was confirmed that, for both types of cues, the reaction times were shorter in the valid than neutral trials (both $ps<.001$), whereas there was no difference between the neutral and invalid trials (both $ps>.1$). The main effect of Cue type indicated that overall the reaction times were shorter after the arrow (mean 264 ms) than gaze (mean 272 ms) cues.

2.2. ERP responses triggered by directional cues

Figs. 3 and 4 show grand average ERP waveforms for the left/right attention-directing arrow and gaze cues, respectively, measured from midline and lateral electrodes located at frontal, central, parietal, and occipital sites. The ERP responses from these electrodes are illustrated as they capture the essential patterns of observed results of the 64-channel recordings. The left and right attention-directing cues did not evoke differential P1 or N1 responses in the posterior channels, consistent with the fact that the low-level visual stimulation of the left and right cues was similar in both visual fields. For the occipital electrodes, the subsequent components were not either affected by the cue direction. As described in the introduction, the attention orienting related effects observed in previous studies have been largest over the lateral occipito-parietal (EDAN) and fronto-central regions (ADAN). In the present data, there also seemed to be an EDAN effect for the arrow cues at the lateral parietal electrodes (P7/P8) starting at about 200 ms post-cue (Fig. 3). For the gaze cues, however, no such effect was observed (Fig. 4). Regarding the somewhat later, more anterior ADAN response, the effects seemed to be small. For the arrow cues, a small difference was visible in the response of the C3 electrode (left hemisphere) between left and right-pointing arrows around 320 ms after the cue presentation. Statistical data analyses were confined to electrode pairs P7/P8 and C3/C4. The data were analyzed in 20-ms time bins between 180 ms and 400 ms post-cue by 3-way repeated measures ANOVAs with Cue type (arrow vs. gaze), Cue direction (left vs. right), and Hemisphere (left vs. right) as independent variables.

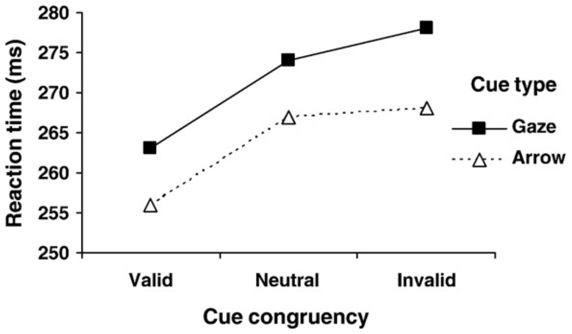

Fig. 2 – Mean reaction times as a function of cue validity and cue type.

In the analyses, the effect of major interest was Cue type × Cue direction × Hemisphere-interaction. For the data recorded from the electrode pair P7/P8, the Cue type × Cue direction × Hemisphere-interaction was significant between 221 and 260 ms, i.e., for the time bins of 221–240 ms and 241–260 [$F(1,16)=4.67$, $p<.05$, $\eta^2_p=.23$ and $F(1,16)=11.3$, $p<.01$, $\eta^2_p=.41$, respectively]. Pairwise comparisons indicated that, for the arrow cues, the brain responses were significantly less positive (shifted in the negative direction) to the contralateral than ipsilateral cues in the left hemisphere [221–240 ms: $t(16)=3.2$, $p<.01$ and 241–260 ms: $t(16)=6.6$, $p<.001$] and marginally in the right hemisphere [$t(16)=1.8$, $p<.1$ and $t(16)=2.0$, $p<.07$]. For the gaze cues, none of the effects was even marginal (all $ps>.2$).

For electrode pair C3/C4, the analyses revealed that the Cue type × Cue direction × Hemisphere was statistically significant for the data from the time bin of 321–340 ms [$F(1,16)=5.6$, $p<.04$, $\eta^2_p=.26$]. Pairwise comparisons showed that the responses were significantly less positive for the contralateral than ipsilateral cues only for the arrow cues in the left hemisphere [$t(16)=2.7$, $p<.02$]. Responses in the right hemisphere to the arrow cues or responses to the gaze cues in either hemisphere were not affected by the cue direction (all $ps>.4$).

2.3. ERP responses triggered by directional vs. non-directional cues

The ERP analysis regarding the responses triggered by directional vs. non-directional cues was also confined to the central and parietal recording sites where effects by directional (left vs. right) cues were observed. Fig. 5 shows grand average ERP waveforms for the directional (collapsed across left and right cues) and non-directional (direct) arrow and gaze cues, respectively, measured from the midline and lateral electrodes located at the central and parietal sites. For both types of cues, directional and non-directional cues elicited differential waveforms at all recording sites. The differences were observed in several time periods distributed over the 500-ms time period between the cue onset and the target onset. The data were analyzed statistically in 20-ms time bins between 100 ms and 500 ms post-cue.

First, the responses measured from the midline (Cz, Pz), centro-lateral (C3, C4), and parieto-lateral (P7, P8) electrodes in each 20-ms time bin were separately analyzed by Cue type (arrow vs. gaze) × Cue directionality (directional vs. non-directional) × Electrode ANOVAs. The effects of Cue directionality and

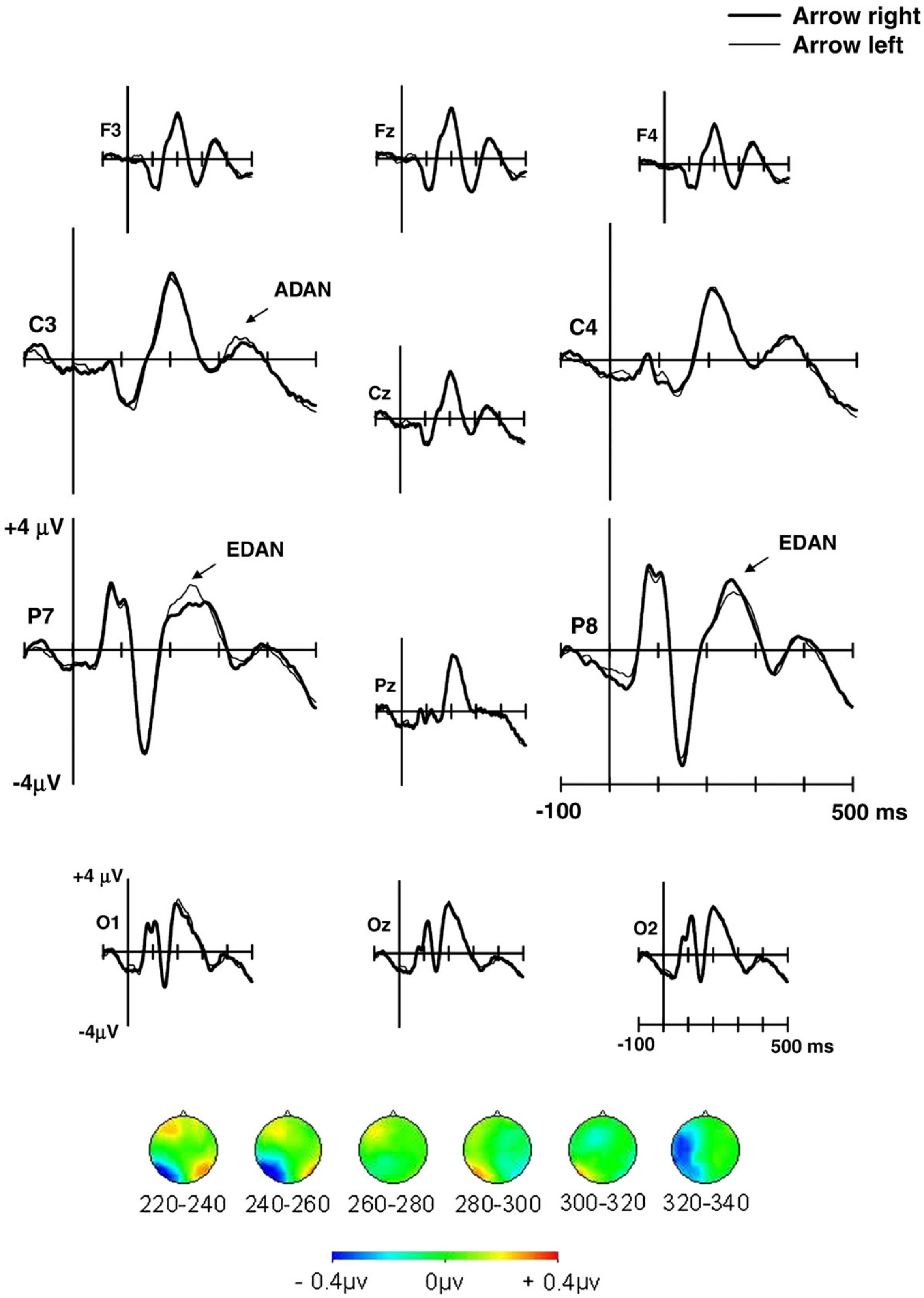

Fig. 3 – Top: Average ERP waveforms at frontal (F3/Fz/F4), central (C3/Cz/C4), parietal (P7/Pz/P8), and occipital (O1/Oz/O2) electrodes elicited by arrows pointing to the left and right. The EDAN and ADAN effects are indicated. Time = 0 ms indicates the cue onset. Bottom: Distribution maps of the mean voltage amplitudes for the left vs. right-pointing arrow (right–left) difference ERPs in time windows 220–240, 240–260, 260–280, 280–300, 300–320, and 320–340 ms post-stimulus.

interaction between Cue directionality and Cue type were of main interest. However, these analyses revealed that the factor of Electrode was also significantly interacting with these effects in several time bins. Therefore, the data were next analyzed separately for each electrode and each time bin by Cue type × Cue directionality ANOVAs.

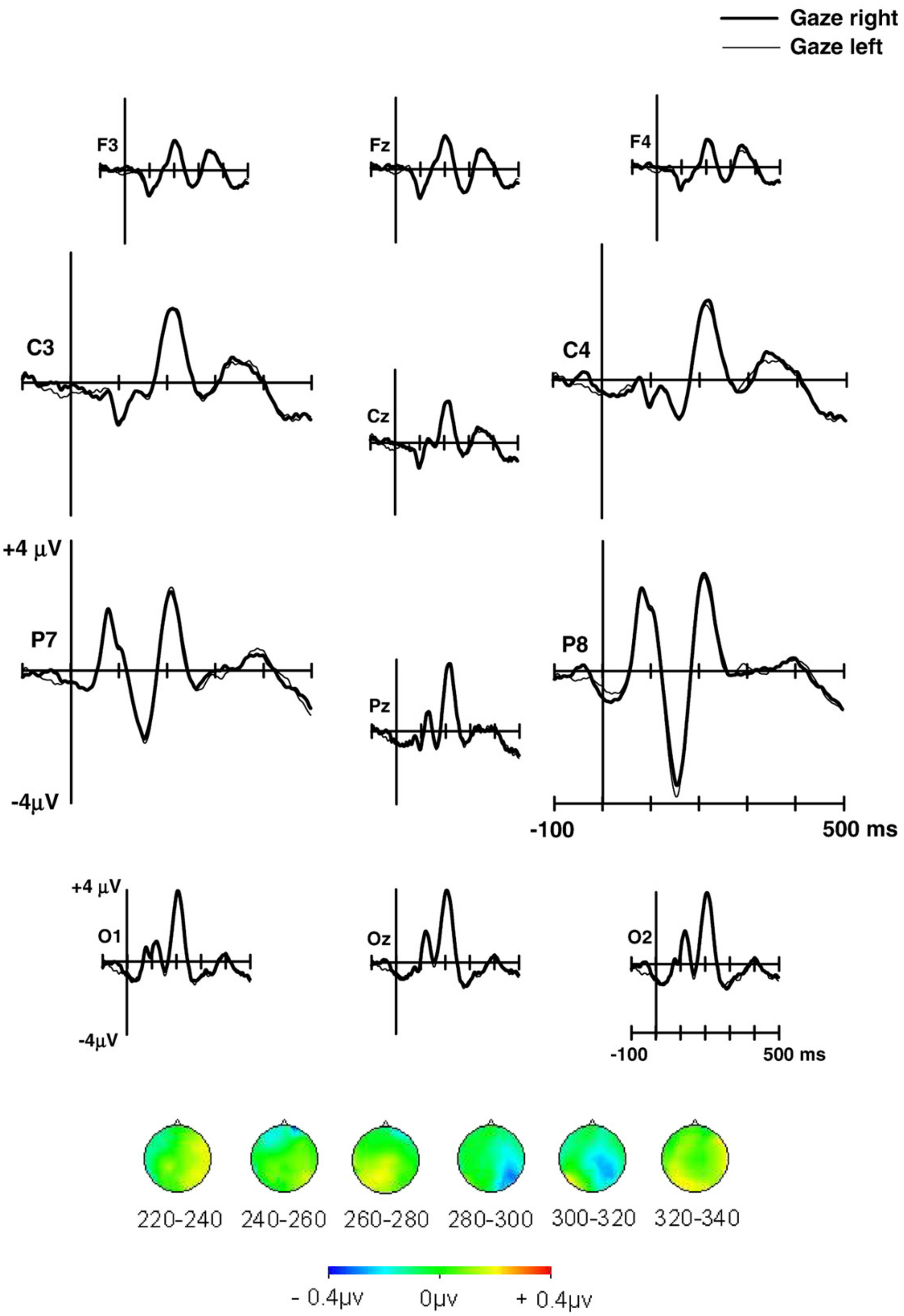

Fig. 4 – Top: Average ERP waveforms at frontal (F3/Fz/F4), central (C3/Cz/C4), parietal (P7/Pz/P8), and occipital (O1/Oz/O2) electrodes elicited by gaze directed to the left and right. Time = 0 ms indicates the cue onset. Bottom: Distribution maps of the mean voltage amplitudes for the left vs. right directed gaze (right–left) difference ERPs in six consecutive 20-ms time windows starting at 220 ms post-stimulus.

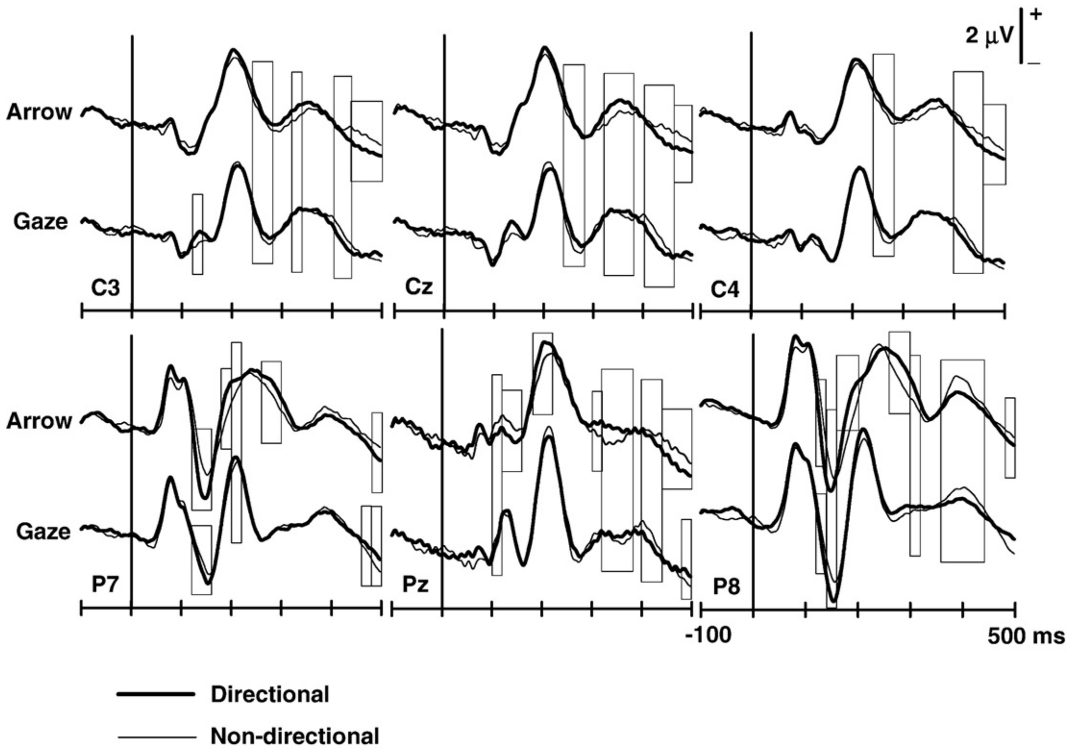

Fig. 5 – Average ERP waveforms at central (C3/Cz/C4) and parietal (P7/Pz/P8) electrodes elicited by directional (left/right) and non-directional (neutral) arrow and gaze cues. The rectangles superimposed on the ERP waveforms indicate the periods of time when the directional and non-directional waveforms differed significantly (for more detailed explanation, see main text). Time = 0 ms indicates the cue onset.

In Fig. 5, the results of the statistical analyses involving the effect of Cue directionality are indicated by rectangles superimposed on the ERP waveforms. A significant ($p<.05$) main effect of Cue directionality (in a 20-ms time window) is indicated by a rectangle crossing the waveforms for both the arrow cues and gaze cues. If the main effect of Cue directionality was qualified by a Cue type × Cue directionality interaction, the effect of directionality was analyzed separately for the arrow and gaze cues. In this case, a rectangle crosses only the waveform where a significant difference in the response between directional and non-directional cues was observed. In a few cases, where the two-way interaction (Cue type × Cue directionality) was significant and the effect of directionality turned out to be significant for both the arrow and gaze cues, there are two separate rectangles for the arrow and gaze cues.

For the central recording sites (C3, Cz, C4), the waveforms for directional cues were shifted in the positive direction relative to the waveforms for non-directional cues starting at around 240 ms post-cue. This applied for both the arrow and gaze cues. The first period of enhanced positivity for directional cues lasted for about 40 ms followed by another starting at 320 ms post-cue and lasting about 60 ms. Approximately 400 ms after the cue onset, the waveforms for non-directional cues became more positive relative to the waveforms for directional cues. For 400 to 460 ms from the cue onset, this was observed for both the arrow and gaze cues, but after that only the arrow cues exhibited this pattern of results. For the lateral parietal recording sites (P7, P8), responses between 120 and 160 ms post-cue (N1 component) were enhanced for the directional compared to non-directional cues. Again, this applied for both the arrow and gaze cues. After 200 ms post-cue, there was indication of enhanced positivity to directional relative to non-directional cues at all parietal channels, although this phenomenon seemed to be clearer for the arrow than gaze cues. After 400 ms post-cue, the waveforms for the non-directional cues became more positive than those for the directional cues. However, towards the end of the analysis period, the waveforms for the directional gaze cues became more positive than those for the non-directional gaze cues.

2.4. *Target-triggered ERP responses*

The amplitudes and latencies for target-triggered P1 and N1 components were inspected from posterior channels. The statistical analyses were confined to parietal (P5/P6) and temporo-parietal (P7/P8) channel pairs where the effects seemed to be most prominent (Fig. 6). The data were subjected to 4-way repeated measures ANOVAs with Cue type (arrow vs. gaze), Cue validity (valid, neutral, invalid), Site (parietal vs. temporo-parietal) and Hemisphere (left vs. right) as independent variables.

For the P1 amplitude data, the analysis revealed a main effect of Hemisphere [$F(1,16)=15.9$, $p<.001$, $\eta_p^2=.50$] and Site × Hemisphere [$F(1,16)=5.0$, $p<.05$, $\eta_p^2=.24$], Cue type × Cue validity [$F(2,32)=5.1$, $p<.02$, $\varepsilon=.83$, $\eta_p^2=.24$], Cue type × Cue validity × Hemisphere [$F(2,32)=3.9$, $p<.04$, $\varepsilon=.97$, $\eta_p^2=.20$]

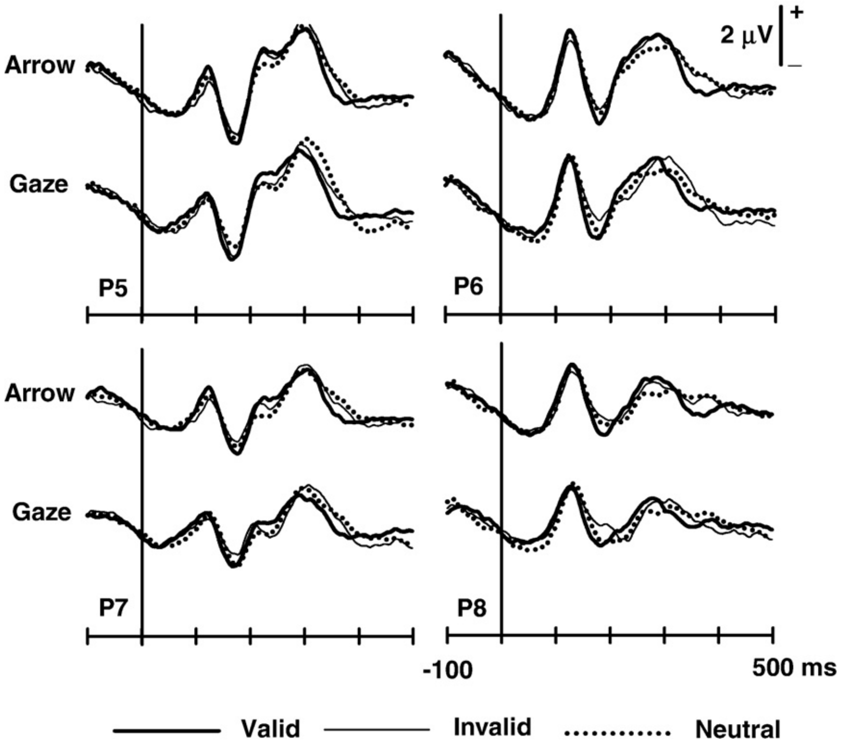

Fig. 6 – Target-triggered average ERP waveforms at four parietal electrodes (P7/P5/P6/P8). ERP responses are depicted for targets preceded by valid, invalid, and neutral arrow and gaze cues. Time = 0 ms indicates the target onset.

interactions. However, when the interactions were further analyzed, there was no effect involving Cue validity for neither the arrow or gaze cues. For the N1 amplitudes, the analysis revealed main effects of Cue type [$F(1,16)=5.6$, $p<.04$, $\eta_p^2=.26$, $M_{arrow}=-2.1$ μV vs. $M_{gaze}=-1.9$ μV], Hemisphere [$F(1,16)=5.3$, $p<.04$, $\eta_p^2=.25$; $M_{left}=-2.2$ μV vs. $M_{right}=-1.7$ μV], Site [$F(1,16)=41.73$, $p<.001$, $\eta_p^2=.72$; $M_{parietal}=-2.2$ μV vs. $M_{temporo\text{-}parietal}=-1.7$ μV], and Cue validity [$F(2,32)=4.3$, $p<.03$, $\varepsilon=.79$, $\eta_p^2=.21$]. None of the interactions was significant. Further post hoc analyses revealed that the N1 amplitude for the valid trials was significantly larger than the N1 amplitude for the invalid (−2.2 μV vs. −1.8 μV, $p<.03$) trials and also marginally larger than the N1 amplitude for the neutral trials (−1.8 μV, $p=.051$), whereas there was no difference between the neutral and invalid trials.

For the P1 latencies, the analysis revealed main effects of Cue type [$F(1,16)=18.4$, $p<.001$, $\eta_p^2=.53$], Hemisphere [$F(1,16)=10.7$, $p<.01$, $\eta_p^2=.40$], and Cue validity [$F(2,32)=6.4$, $p<.01$, $\varepsilon=.95$, $\eta_p^2=.29$]. These effects were qualified by Hemisphere × Cue type [$F(1,16)=4.7$, $p<.05$, $\eta_p^2=.23$] and Site × Cue validity [$F(2,32)=3.6$, $p<.01$, $\varepsilon=.84$, $\eta_p^2=.19$] interactions. Further analyses revealed that the effect of Cue validity was significant at both the parietal [$F(2,32)=8.1$, $p<.001$, $\varepsilon=.92$, $\eta_p^2=.34$] and temporo-parietal [$F(2,32)=4.0$, $p<.03$, $\varepsilon=.92$, $\eta_p^2=.20$] recording sites. At the parietal recording site, the P1 latencies were significantly shorter for the valid (122 ms) than for the invalid (126 ms) and neutral (126 ms) trials (both $ps<.01$) and, at the temporo-parietal sites, the P1 latencies were significantly shorter for the valid (125 ms) than for the invalid (128 ms) trials ($p<.02$). For the N1 latencies, the analysis revealed a main effect of Hemisphere [$F(1,16)=15.4$, $p<.001$, $\eta_p^2=.49$] and Cue type × Cue validity interaction [$F(2,32)=4.3$, $p<.03$, $\varepsilon=.97$, $\eta_p^2=.21$]. However, further analyses revealed that the effect of validity was not significant neither for the arrow or gaze cues (averaged over Site and Hemisphere).

3. Discussion

We measured attention orienting related ERP responses and manual reaction times while the participants were performing a standard spatial cuing task with centrally presented, directional and non-directional arrow or gaze cues followed by laterally presented targets. The behavioral and target-triggered ERP data showed that both valid arrow cues and valid gaze cues speeded and enhanced the responses to targets as compared to respective invalid cues. However, the cue-triggered ERP data indicated that the attention orienting related ERP effects elicited by the arrow and gaze cues were different at the lateral parietal and fronto-central electrode sites. First and most importantly, the arrow cues elicited the typical cue direction-related ERP effects (i.e., EDAN and ADAN), whereas the gaze cues did not. Second, although both cues elicited general attention orienting related effects, there were differences in these effects between the arrow and gaze cues. We interpret these results to provide further support for earlier behavioral (e.g., Friesen et al., 2004; Langdon and Smith, 2005) and neuroimaging (e.g., Hietanen et al., 2006) studies indicating that automatic orienting of attention by arrow cues and gaze cues are mediated by different neural mechanisms.

3.1. *EDAN and ADAN*

Earlier studies have shown that centrally presented attention-directing arrow cues elicit a so-called “early directing attention negativity” effect (EDAN) observed in occipital–parietal channels between 200 and 400 ms after cue onset. This effect is recorded over the hemisphere contralateral to the direction indicated by the cue (Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Talsma et al., 2005, Van der Lubbe et al., 2006; Yamaguchi et al., 1994). Compatible with the earlier studies and our hypotheses, the present results showed that the arrow cues elicited a clear EDAN effect over parietal channels. The ERP responses within a time window of 220–260 ms after the presentation of the arrow cue were shifted in the negative direction for the arrow cues pointing to the direction which was contralateral to the recorded hemisphere as compared to arrow cues with ipsilateral direction. Unexpectedly, for the gaze cues, we could not find any EDAN effect at all. It has been proposed that the EDAN reflects the shifts of visuospatial attention (Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000; Yamaguchi et al., 1994). This proposition is supported by the localization of the EDAN maximum over the occipito-parietal sites, i.e., over those areas postulated to be central in re-directing of visuospatial attention. Corbetta and Shulman (2002) have suggested that visual attention is controlled by two partially segregated neural systems: voluntary control of visuospatial attention is governed by a network consisting of dorsal parietal and superior frontal cortices (a dorsal fronto-parietal network), whereas reflexive control of attention involves neural systems in the temporo-parietal and inferior frontal cortices (a ventral fronto-parietal network). The results from a previous neuroimaging study (Hietanen et al., 2006) with the same directional cues as in the present study were interpreted to lend support for a view that attention orienting by arrow cues relies more strongly on the dorsal network than does the attention orienting by gaze cues. Thus, the present ERP results can be interpreted to suggest that the EDAN reflects activation of the dorsal (voluntary) rather than the ventral (reflexive) attention orienting networks and, therefore, the EDAN effect was not observed for the gaze cues. It is possible that the lack of any EDAN effects for the gaze cues in the posterior channels may be explained by the disadvantageous location (orientation of the signal sources) of the mechanisms of gaze-cued orienting in order to be detected by the EEG and/or by the greater dependence of gaze cuing on subcortical mechanisms (see below).

The second attention orienting related effect, the anterior directing attention negativity (ADAN) was weak in the present data. The ADAN is typically observed at around 300–500 ms after the cue onset at fronto-central channels (Hopf and Mangun, 2000; Nobre et al., 2000; Talsma et al., 2005; Van der Lubbe et al., 2006). The present results showed a significant ADAN response for the arrow cues only in the left hemisphere and only for a short time period between 321 and 340 ms after the cue onset. It should be noted, however, that the ADAN has not been observed in all the previous studies (i.e., Harter et al., 1989; Yamaguchi et al., 1994) and, in general, its characteristics are much more variable between different studies as compared to those of the EDAN. Moreover, in most of the previous studies reporting the ADAN, the cues were predictive (Nobre et al., 2000; Talsma et al., 2005; Van der Lubbe et al., 2006), whereas in the present study they were non-predictive.

The ADAN is suggested to reflect the activity of the frontal attention-controlling areas. Again, the fact that the minor ADAN response was observed only for the arrow cues is compatible with the previous imaging data (Hietanen et al., 2006) which showed that arrow cuing but not gaze cuing activated the frontal attention and eye movement controlling regions such as frontal eye fields (FEF) and supplementary eye fields (SEF). However, it must be noted that, in the imaging study by Hietanen et al., arrow cuing activated the right FEF and SEF, whereas in the present study, the ADAN effect for the arrow cues was observed in responses measured from a left-sided electrode. The analysis of the ERP responses to directional vs. non-directional arrow and gaze cues – an analysis which resembles that used in the previous imaging study comparing hemodynamic responses for directional vs. non-directional cuing – also showed that the effect was bilateral and, if anything, stronger in the left than right recording sites. At the moment, we do not have an explanation for this laterality difference between the results of the present study and the fMRI study by Hietanen et al. Of course, due to the poor spatial resolution of the ERPs, the comparison of the results regarding signal localization between imaging and electrophysiological studies is problematic. In any case, the FEF is commonly regarded to be a part of a neural network involved in voluntary shifts of covert attention (Corbetta and Shulman, 2002, Kastner and Ungerleider, 2000). Thus, the present finding of frontally measured responses to arrow but not to gaze cues is compatible with the suggestions that arrow-triggered shifts of attention activate the voluntary attention shifting mechanisms more than do the gaze-triggered shifts of attention, and suggest that the ADAN results from activation of the dorsal fronto-parietal (voluntary) attention orienting mechanisms.

It would be interesting to contemplate the present results against those earlier results which have compared attention orienting related ERP responses elicited by arrows and peripheral illumination changes, a cue classically considered to elicit reflexive shifts of attention. However, the issue of comparison is complicated by the fact that the peripherally presented cues elicit, of course, enhanced responses in the contralateral hemisphere just because of the lateral presentation of the cues. Yamaguchi et al. (1994) investigated attention orienting related ERP responses both to centrally presented symbolic and peripherally presented illumination change cues. As already noted, for the arrow cues, they observed a posterior EDAN at around 240–380 ms, but also, for the peripheral cues, the ERPs were more negative in the hemisphere contralateral to the cue at all sites between 140 and 200 ms. Although Yamaguchi et al. considered this latter negativity to be an enhancement of the N1 component reflecting the occurrence of the illumination changes (cues) in the visual periphery they, nevertheless, considered it possible that it could have also reflected neural processes involved in attention orienting. Obviously, verification of this possibility is difficult. In the present study, the gaze and arrow cues were both centrally presented, simple schematic drawings which did not differ widely in their low-level visual features such as mean luminosity or contrast density, and which did not elicit differential early responses (P1 and N1) in the left and right hemispheres. Accordingly, the comparison of the neural responses triggered by these two types of schematic cues is not confounded by such factors which complicate the comparison of responses elicited by central arrow cues and peripheral illumination change cues as described above. Therefore, in light of the present results we are inclined to suggest that reflexive orienting of attention does not result in the EDAN and ADAN effects.

Recently, Nummenmaa and Hietanen (2006) provided evidence for the reflexive nature of gaze-cued orienting measuring saccadic curvature while participants were instructed to make vertical saccades from a central fixation to targets appearing abruptly at the visual periphery. Centrally presented schematic faces with averted gaze (similar to those in the present study) or peripheral boxes were presented as distractors before or simultaneously with the imperative signal. The results showed that both gaze and peripheral distractors caused the saccades to curve away from the distractor direction. As covert orienting of spatial attention by irrelevant peripheral distractors is known to activate the oculomotor system and influence the curvature of orthogonal saccades (Doyle and Walker, 2001; Godijn and Theeuwes, 2004, Experiment 1), the results by Nummenmaa and Hietanen suggested that gaze-cued attention orienting also involves the functioning of subcortical oculomotor systems associated with reflexive orienting. Thus, one possible explanation for the lack of EDAN and ADAN effects for gaze cues could be that orienting of attention by gaze cues is highly dependent on subcortical attention orienting systems, and this activity is not reflected in the ERP measures.

3.2. *Does EDAN reflect the control of attention orienting?*

Interestingly, not all the researchers have been convinced that the EDAN reflects attention orienting related processes. Van Velzen and Eimer (2003) provided evidence that the EDAN does not reflect the orienting of attention but selection of the side of the cue stimulus (e.g., an arrow head) signaling the to-be-attended side. Van Velzen and Eimer pointed out that in earlier studies reporting the EDAN, the arrow cues were not symmetrical with respect to the fixation. In the arrows pointing to the right, the arrow head was located to the right of fixation and, in the arrows pointing to the left, the arrow head was located to the left of fixation. Even in the study by Nobre et al. (2000), in which the cue was composed of two differently colored arrowheads arranged to form a bi-colored diamond shape, symmetrical with respect to the fixation, the cue directing attention to the left or right was always on the left or right side of the diamond shape (the relevant cue was either the green- or red-colored side of the diamond). Thus, according to Van Velzen and Eimer, it was possible that the EDAN recorded in each hemisphere did not reflect processes involved in orienting of attention to the contralateral side of the visual field, but rather the detection and selection of the task-relevant side of the cue.

In order to provide evidence for this hypothesis, Van Velzen and Eimer (2003) used two types of cues. Compatible cues were composed of two simultaneously presented arrow-heads arranged in such a way that the left-pointing arrow was located to the left and the right-pointing arrow was located to the right of fixation (like in the study by Nobre et al.). Instead, in incompatible cues both arrows were pointing to the fixation. In other words, the left-pointing arrow was located to the right of fixation and the right-pointing arrow was located to the left of fixation. The arrows were differently colored and the participants were instructed before the task whether the red or blue arrows indicated the attended location. The results indicated that an EDAN contralateral to the direction of an attentional shift (and contralateral to the relevant side of the cue) was observed with compatible cues, whereas a reversed EDAN was observed with incompatible cues. With incompatible cues, an enhanced negativity was elicited ipsilateral to the direction of the attentional shift (but, again, contralateral to the relevant side of the cue). Thus, the results seemed to provide evidence for the proposed hypothesis.

However, both in the study by Nobre et al. (2000) as well as that by Van Velzen and Eimer (2003), the participants were instructed that only one of the two differently coloured arrows was to-be-attended and was relevant for their task performance. Therefore, in the Van Velzen and Eimer study, the directional cues were not symmetrical either but contained relevant and irrelevant parts. It is possible that upon appearance of the bi-colored cue stimulus, the designated color had an effect on attention orienting before orienting based on the directional meaning of the arrow cue, and the reported EDAN effect reflected color-cued attention orienting and not arrow-cued attention orienting. Instead, in the present study, the arrow cues had heads pointing to the same direction at both ends of a line and, therefore, the cues were symmetrical and there were not any relevant and irrelevant parts in the cue stimuli. Still, as described, our results showed an EDAN contralateral to the direction indicated by the cue and alleged direction of attentional shift. Moreover, even if the above line of argument was not accepted and the EDAN was claimed to reflect some processes related to the detection and selection of the task-relevant side of the cue and not to the attention orienting, it would be very difficult to explain then, why this did not happen with the gaze cues.

3.3. *ERPs to directional and non-directional cues*

In the present study, we also compared ERPs to directional (left and right combined) and non-directional (neutral) cues. These analyses revealed two interesting findings. First, although the EDAN and ADAN effects were observed only for the arrow but not for the gaze cues, the directional vs. non-directional cues elicited differential ERP responses for both the arrow and gaze cues. This indicates that gaze cues also initiated attention orienting related brain responses even though they were not observed in the direction-specific EDAN and ADAN effects. The ERPs to directional vs. non-directional cues were, nevertheless, different between the arrow and gaze cues. After initial positive shift to directional relative to non-directional cues, the effect reversed for both types of cues (positive shift to non-directional cues) at around 400 ms post-cue, a result also reported by Talsma et al. (2005) for the arrow cues. However, the effect extended to the end of the analysis period for the arrow cues, but disappeared or even reversed (at parietal channels) for the gaze cues. Also, at the parietal channels, the early positive shift for directional relative to non-directional cues was more pronounced for the arrow than gaze cues.

Second, the results showed that there were differences already in the early visual N1 responses to directional vs. non-directional cues. Earlier studies investigating the effects of gaze direction on early visual, face-sensitive ERP responses have yielded somewhat inconsistent results. For example, Taylor et al. (2001b) did not find any effects of gaze direction on N1 (N170, the so-called early face specific component, Bentin et al., 1996) responses to full faces, whereas Watanabe et al. (2002) reported some evidence for larger N1 amplitudes (N190, in their study) to averted than to straight eyes measured at the right temporal recording site. One plausible reason for the clear effects of gaze and arrow direction on the N1 responses observed in the present study is that, in the present experiment, the gaze and arrow direction-related responses were measured in the context of an attention orienting task. Although the cues were non-predictive, it can be envisaged that in the present experiment, the gaze and arrow direction information was more relevant to the participants than in the tasks requiring only passive observation of the gaze stimuli (Watanabe et al., 2002) or detection of non-face targets (Taylor et al., 2001b). This enhanced relevance of the gaze and arrow direction information might have attributed to the finding of differential N1 responses to directional vs. non-directional gaze and arrow cues. The larger N1 amplitudes for the directional than non-directional cues may reflect the decoding of left–right directional information from these cues.

3.4. *Electrophysiological and behavioral responses to targets*

In general, the present results were in concordance with the earlier studies investigating the ERPs to targets preceded by valid and invalid arrow (Eimer, 1997; Hopf and Mangun, 2000; Luck et al., 1994; Mangun and Hillyard, 1991; Nobre et al., 2000; Talsma et al., 2005) and gaze cues (Schuller and Rossion, 2001, 2004, 2005). The target-triggered ERPs indicated no effect of validity on the P1 amplitudes but the N1 amplitudes were significantly larger for the valid than for the invalid trials. Notably, the statistical analysis suggested this effect was similar for the arrow and gaze cues. Similarly, the P1 latencies were significantly shorter for the valid than invalid trials for both the arrow and gaze cues. Instead, for the N1 latencies, no effect of validity was observed. In sum, the present results suggest that, although the mechanisms subserving arrow-triggered and gaze-triggered attention orienting might be different, the effects of resulting attention orienting on the processing of incoming visual information are similar.

Compatible with the electrophysiological data, the behavioral results showed a cuing effect for both gaze and arrow cues. There are two interesting findings in the behavioral results. First, for both gaze and arrow cues, the RTs in the neutral cuing condition were longer than those in the valid condition but did not differ from those in the invalid condition. It has been suggested that, for gaze cuing studies, the straight gaze might not be an optimal stimulus to be used as a neutral baseline cue because a straight gaze (eye contact) might result in attentional dwelling on this cue and disproportionately lengthens the RTs to the targets following these neutral stimuli. This, in turn, would inflate the RT difference between neutral and invalid gaze cue-conditions. Senju and Hasegawa (2005) reported longer behavioral RTs to laterally presented targets after straight gaze than averted gaze or eyes shut-conditions and suggested that a straight gaze captures the perceiver's attention (see also Von Grünau and Anston, 1995). However, in their experiment, the head stimuli were slightly laterally rotated and, therefore, the eyes were rotated (with respect to the head) in the straight gaze-condition. Moreover, in the averted gaze-condition, the eyes looked down revealing very little of the light (sclera) and dark (iris/pupil) areas of the eyes. For these reasons, in Senju's and Hasegawa's study, the comparison between straight gaze and averted gaze/eyes shut conditions is problematic and hardly comparable to straight gaze and averted gaze-conditions when these cues are embedded in a frontal view of a face.

In the present study, we were able to compare the pattern of behavioral RTs for valid, neutral, and invalid trials between two types of cues: gaze and arrows. If attentional dwelling had occurred in the context of neutral gaze cues, the RTs on these trials should have been closer to the RTs on invalid gaze trials (or even longer than those) as compared to the RT difference between neutral and invalid arrow cues. However, the results indicated a similar pattern of RT results between the cuing conditions for both the gaze and arrow cues. We interpret this result as speaking against a possibility that a straight gaze results in differential attention dwelling as compared to averted gaze. Regarding the pattern of RTs between the conditions of gaze validity, the present result replicated earlier findings for gaze cuing (Friesen and Kingstone, 1998; Hietanen and Leppänen, 2003, Experiments 1–4; Hietanen and Yrttimaa, 2005). The difference in the results between the studies mentioned above and those by Senju and Hasegawa (2005) are not explained either by the fact that Senju and Hasegawa used photographs of a real person as a cue stimulus, whereas simple schematic faces were used in the other studies. In one of their experiments, Hietanen and Leppänen (2003, Experiment 6, task 2) also used photographs of faces as cues, and in that experiment the results indicated, in fact, that the RTs for the neutral trials located between (and differed significantly from) those for the valid and invalid trials. Earlier Langdon and Smith (2005) have also compared the attentional effects of gaze (using photographs of faces as cues) and arrow cues and their results did not provide any evidence that direct gaze would capture attention. Their results reported quite the contrary: valid arrow cues facilitated RTs with respect to a neutral cue, but invalid arrows did not lead to inhibition, whereas valid and invalid gaze cues result in both reaction time facilitation and inhibition, respectively. In sum, we suggest that the majority of the empirical evidence at the moment speaks against the view that straight gaze cues would hold the attention and lengthen the RTs to peripheral targets in a spatial attention paradigm.

The second interesting finding in the behavioral results was that the main effect of cue type indicated significantly shorter reaction times after the arrow than gaze cues. This result replicates earlier findings with the same stimuli (Hietanen et al., 2006). Following the line of reasoning presented in the paragraph above, we are tempted to suggest that the face cues – irrespective of the gaze direction – could result in enhanced attentional dwelling relative to the arrow cues, which would delay the detection of the targets. Vlamings et al. (2005) and Friesen et al. (2004) have also reported shorter reaction times after the arrow than gaze cues. However, there are also other kinds of results. Ristic et al. (2002) did not find an effect of cue type on the RTs and Quadflieg et al. (2004, Exp. 3), in fact, reported shorter RTs after gaze than arrow cues (eyes vs. arrows embedded in a glove). Thus, considering these contradictory results we are cautious in suggesting that the overall longer RTs after gaze than arrow cues observed in the present and earlier studies may be indicative of attentional capture by the face cues. Moreover, in the present study, the target-triggered ERP data showed a significant main effect of cue type on the P1 latencies indicating that the P1 latency was 2 ms shorter for the gaze (124 ms) than arrow (126 ms) cues. Thus, the P1 latency data and the behavioral RT data indicated a reverse order for speed of target processing after arrow and gaze cues. This suggests that if the targets are processed faster after the gaze than arrow cues by the time reflected in P1 latencies, the processing, thereafter, is slower for targets following the gaze than arrow cues. Clearly, these issues remain open for future studies.

3.5. Conclusions

In sum, the present ERP study provided support for a view that automatic orienting of visual attention is realized by different mechanisms when the shifts of attention are triggered by non-predictive gaze cues and arrow cues. Together with earlier behavioral (Friesen et al., 2004; Langdon and Smith, 2005) and neuroimaging (Hietanen et al., 2006) evidence these results provide further support for the notions that another person's gaze triggers a special type of automatic shifts of visual attention. In the present study, the arrow cues elicited a prominent, posterior attention orienting related negativity (EDAN) and a weaker anterior negativity (ADAN) observed in many other studies, whereas the gaze cues did not trigger these kinds of effects at all. The present results complemented the previous neuroimaging results by suggesting that the involvement of differential neural mechanisms for gaze-cued and arrow-cued orienting can be observed at around 200 ms after the cue onset. Both types of cues resulted in electrophysiological and behavioral cuing effects. As both types of cues were centrally presented, relatively similar, simple drawings, comparison of the brain responses elicited by these two types of cues are not complicated by factors related to gross differences in the low-level visual features between the cues. It is suggested that the EDAN and ADAN reflect the functioning of the dorsal fronto-parietal attention orienting systems associated with voluntary shifts of attention (Corbetta and Shulman, 2002). Thus, arrow-cued shifts of attention rely on the workings of this mechanism, whereas gaze-cued attention relies on the ventral fronto-parietal (Corbetta and Shulman, 2002) and oculomotor (Nummenmaa and Hietanen, 2006) attention orienting systems associated with involuntary shifts of attention.

4. Experimental procedures

4.1. Participants

Seventeen introductory psychology students (14 females, age range 19–26 years, mean 22.2 years) took part in the experiment. All participants reported normal or corrected to normal vision. They were unaware of the purpose of the experiment. An informed, written consent was obtained from each participant. From the original 19 participants, 2 had to be discarded. One participant's low visual acuity was not corrected and in another participant's EEG recording the electrode impedances were not at a satisfying level during the whole recording period.

4.2. Stimuli

Two kinds of cue stimuli were used in the experiment. They were either pictures of a "traffic sign" or a schematic face (see Fig. 1). The traffic signs consisted of a circle subtending 10° centered on the screen, a horizontal line subtending 6.7° centered on the central vertical axis, and the arrow tips or short vertical lines (.7° vertically) at the beginning and at the end of the horizontal line. The arrow tips pointed to left or right. The face displays consisted of black line drawings of a round schematic face subtending 10° and centered on the middle of the screen. The eyes subtended 1.5°, were located on the central horizontal axis, and were 4.0° apart across the central vertical axis. Black-filled circles inside the eyes represented pupils. The pupils subtended .7°, were centered vertically to the eyes, and were just touching left or right side of the eye or were centered in the eyes. The target stimulus demanding response was a black asterisk (diameter .4°) presented 7° to the left or right of a fixation cross (diameter .4°) centered on the screen. The stimuli were presented on the computer screen (Nokia 930C 17 inch monitor, 75 Hz refresh rate). Stimulus presentation was controlled by Neuroscan Stim software running on a desktop computer.

An experimental trial consisted of the following events: First, a fixation cross appeared at the center of the screen for 1000 ms. Next, the fixation cross was replaced by a cue stimulus, followed by a target stimulus which appeared either validly (on the same side), invalidly (on the opposite side), or neutrally (after a straight line or a face looking forward) with respect to the direction indicated by the cue. The stimulus-onset-asynchrony (SOA) between the cue and target was 500 ms. The cue and the target remained on the screen until the participant's response. The next trial was presented after 500 ms from the response.

4.3. Procedure

Upon arriving in the laboratory, participants gave a written informed consent. The purpose of the study was explained to the participants. In instruction, the cues were introduced as traffic signs with arrows and faces. Participants were seated in a comfortable chair in a dimly lit laboratory room, at a distance of 77 cm from the computer screen. A response box (Neuroscan Stim System Switch Response Pad P/N 1141) was given to them, and they were familiarized with the task.

The experiment consisted of 10 blocks of trials, 5 arrow-cue and 5 face-cue blocks. There was a short rest period between the blocks. Each block was randomly composed of 30 valid, 30 invalid, and 30 neutral trials. The blocks also included catch trials where no target was presented after the cue. Blocks of arrows and blocks of faces were alternately presented. Half of the participants started with a block of arrows and half of them with a block of faces. Participants were asked to press a response key using their dominant hand when they detected the appearance of the target. No discrimination was required. They were asked to respond as fast as possible and to refrain from pressing the key on catch trials. Catch trials made up 10% of the total number of trials in each block. On catch trials, the next trial started 1000 ms after the presentation of the cue stimulus. Catch trials were presented in order to maintain the attention of the participants during the experiment and to prevent anticipatory key presses. 18 practice trials were run before starting the experiment. It was emphasized that the arrow or gaze direction did not predict the side on which the reaction signal would appear.

4.4. *EEG recordings*

Continuous EEG was recorded using 64 electrodes mounted in an elastic cap (Electro-Cap International, Inc.) and referenced to the tip of the nose. Vertical (VEOG) and horizontal (HEOG) electro-oculogram was recorded with bipolar channels from sites above and below the midpoint of the left eye and beside the outer canthi of each eye. Mild skin abrasion was used to reduce the electrode impedances below 5 kΩ. The EEG was band-pass filtered from .05 to 100 Hz, amplified with a gain of 500, and stored on a computer disk at the sample rate of 1000 Hz (Syn-Amps 4.3, Neuroscan, Inc.).

4.5. *Data analysis*

The continuous EEG signal was corrected for blink artifact using an eye movement reduction algorithm (Semlitsch et al., 1986) and segmented to two 600-ms epochs: one starting 100 ms prior to the presentation of the cue stimulus and another starting 100 ms prior to the target. Epochs were digitally filtered (low pass = 20 Hz, high pass = 2 Hz) and baseline-corrected against the mean voltage during the 100-ms prestimulus period. Baseline-corrected epochs were visually scanned for saccades and other visible artifacts, and if found, the epoch was removed from further analysis. Average waveforms for each individual participant within each experimental condition were calculated from artifact-free trials. For the cue-triggered epochs, statistical analyses were targeted at examining attention related effects over posterior (EDAN) and anterior (ADAN) brain regions. The mean amplitude of the ERP activity was determined in 20-ms time windows from 180 to 400 ms at selected posterior (P7/P8) and anterior (C3/C4) recording sites. These electrode sites were selected based on visual inspection of the grand average waveforms and to cover the scalp regions where attention related effects have been found in previous ERP studies (e.g., Talsma et al., 2005). For the target-triggered epochs, peak amplitudes and peak latencies were identified for P1 (within time window of 105–145 ms) and N1 (140–200 ms) components.

Acknowledgments

We thank Riina Meriläinen-Juurikka and Sini Salvisto for their help in data collection.

REFERENCES

Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Nakachi, R., Kashima, H., 2006a. A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion Neuropsychologia 44, 161–170.

Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Umeda, S., Kashima, H., 2006b. Gaze but not arrows: a dissociative impairment after right superior temporal gyrus damage. Neuropsychologia 44, 1804–1810.

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.

Barrett, L.F., Tugade, M., Engle, R.W., 2004. Individual differences in working memory capacity and dual-process theories of mind. Psychol. Bull. 130, 553–573.

Bentin, S., Allison, T., Puce, A., Perez, E., McCarthy, G., 1996. Electrophysiological studies of face perception in humans. J. Cogn. Neurosci. 8, 551–565.

Calder, A.J., Beaver, J.D., Winston, J.S., Dolan, R.J., Jenkins, E., Eger, E., Henson, R.N.A., 2007. Separate coding of different gaze direction in the human superior temporal sulcus and inferior parietal lobule. Curr. Biol. 17, 20–25.

Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat. Rev., Neurosci. 3, 201–215.

Doyle, M.C., Walker, R., 2001. Curved saccade trajectories: voluntary and reflexive saccades curve away from irrelevant distractors. Exp. Brain Res. 139, 333–344.

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., Baron-Cohen, S., 1999. Gaze perception triggers reflexive visuospatial orienting. Vis. Cogn. 6, 509–540.

Egeth, H.E., Yantis, S., 1997. Visual attention: control, representation and time course. Annu. Rev. Psychol. 48, 269–297.

Eimer, M., 1997. Uninformative symbolic cues may bias visual–spatial attention: behavioral and electrophysiological evidence. Biol. Psychol. 46, 67–71.

Friesen, C.K., Kingstone, A., 1998. The eyes have it: reflexive orienting is triggered by nonpredictive gaze. Psychon. Bull. Rev. 5, 490–493.

Friesen, C.K., Ristic, J., Kingstone, A., 2004. Attentional effects of counterpredictive gaze and arrow cues. J. Exp. Psychol. Hum. Percept. Perform. 30, 319–329.

Godijn, R., Theeuwes, J., 2004. The relationship between inhibition of return and saccade trajectory deviations. J. Exp. Psychol. Hum. Percept. Perform. 30, 538–554.

Harter, M.R., Miller, S.L., Price, N.J., LaLonde, M.E., Keyes, A.L., 1989. Neural processes involved in directing attention. J. Cogn. Neurosci. 1, 223–237.

Hietanen, J.K., 1999. Does your gaze direction and head orientation shift my visual attention? Neuroreport 10, 3443–3447.

Hietanen, J.K., Leppänen, J.M., 2003. Does facial expression affect attention orienting by gaze direction cues? J. Exp. Psychol. Hum. Percept. Perform. 29, 1228–1243.

Hietanen, J.K., Nummenmaa, L., Nyman, M.J., Parkkola, R., Hämäläinen, H., 2006. Automatic attention orienting by social and symbolic cues activate different neural networks: an fMRI study. Neuroimage 33, 406–413.

Hietanen, J.K., Yrttimaa, K., 2005. Where a person with a squint is actually looking: gaze-cued orienting in crossed eyes. Vis. Cogn. 12, 117–126.

Hoffman, E.A., Haxby, J.V., 2000. Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat. Neurosci. 3, 80–84.

Hommel, B., Pratt, J., Colzato, L., Godijn, R., 2001. Symbolic control of visual attention. Psychol. Sci. 12, 360–365.

Hooker, C.I., Paller, K.A., Gitelman, D.R., Parrish, T.B., Mesulam, M.-M., Reber, P.J., 2003. Brain networks for analyzing eye gaze. Cogn. Brain Res. 17, 406–418.

Hopf, J.-M., Mangun, G.R., 2000. Shifting visual attention in space: an electrophysiological analysis using high spatial resolution mapping. Clin. Neurophysiol. 111, 1241–1257.

Jonides, J., 1981. Voluntary versus automatic control over the mind's eye's movement. In: Long, J.B., Baddeley, A.D. (Eds.), Attention and Performance IX. Erlbaum, Hillsdale, NJ, pp. 187–203.

Kastner, S., Ungerleider, L.G., 2000. Mechanisms of visual attention in the human cortex. Annu. Rev., Neurosci. 23, 315–341.

Kingstone, A., Tipper, C., Ristic, J., Ngan, E., 2004. The eyes have it!: an fMRI investigation. Brain Cogn. 55, 269–271.

Langdon, R., Smith, P., 2005. Spatial cueing by social versus non-social directional signals. Vis. Cogn. 12, 1497–1527.

Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., Hawkins, H.L., 1994. Effects of spatial cuing on luminance detectability: psychophysical and electrophysiological evidence for early selection. J. Exp. Psychol. Hum. Percept. Perform. 20, 887–904.

Mangun, G.R., Hillyard, S.A., 1991. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual–spatial priming. J. Exp. Psychol. Hum. Percept. Perform. 17, 1057–1074.

Nobre, A.C., Sebestyen, G.N., Miniussi, C., 2000. The dynamics of shifting visuospatial attention revealed by event-related potentials. Neuropsychologia 38, 964–974.

Nummenmaa, L., Hietanen, J.K., 2006. Gaze distractors influence saccadic curvature: evidence for the role of the oculomotor system in gaze-cued orienting. Vis. Res. 46, 3674–3680.

Perrett, D.I., Hietanen, J.K., Oram, M.W., Benson, P.J., 1992. Organization and functions of cells responsive to faces in the temporal cortex. Proc. Phil. Trans. R. Soc. Lond. Series B, 335, 23–30.

Pelphrey, K.A., Viola, R.J., McCarthy, G., 2004. When strangers pass: processing of mutual and averted social gaze in the superior temporal sulcus. Psychol. Sci. 5, 598–603.

Posner, M.I., 1980. Orienting of attention. Q. J. Exp. Psychol. 32, 3–25.

Quadflieg, S., Mason, M.F., Macrae, C.N., 2004. The owl and the pussycat: gaze cues and visuospatial orienting. Psychon. Bull. Rev. 11, 826–831.

Ristic, J., Friesen, C.K., Kingstone, A., 2002. Are eyes special? It depends on how you look at it. Psychon. Bull. Rev. 9, 507–513.

Schuller, A.-M., Rossion, B., 2001. Spatial attention triggered by eye gaze increases and speeds up early visual activity. Neuroreport 12, 2381–2386.

Schuller, A.-M., Rossion, B., 2004. Perception of static eye gaze direction facilitates subsequent early visual processing. Clin. Neurophysiol. 115, 1161–1168.

Schuller, A.-M., Rossion, B., 2005. Spatial attention triggered by eye gaze enhances and speeds up visual processing in upper and lower visual fields beyond early visual processing. Clin. Neurophysiol. 116, 2565–2576.

Semlitsch, H.V., Anderer, P., Schuster, P., Presslisch, O., 1986. A solution for reliable and valid reduction of ocular artifacts applied to the P300 ERP. Psychophysiology 23, 695–703.

Senju, A., Hasegawa, T., 2005. Direct gaze captures visuospatial attention. Vis. Cogn. 12, 127–144.

Talsma, D., Slagter, H.A., Nieuwenhuis, S., Hage, J., Kok, A., 2005. The orienting of visuospatial attention: an event-related brain potential study. Cogn. Brain Res. 25, 117–129.

Taylor, M.J., George, N., Ducorps, A., 2001a. Magnetoencephalographic evidence of early processing of direction of gaze in humans. Neurosci. Lett. 316, 173–177.

Taylor, M.J., Itier, R.J., Allison, T., Edmonds, G.E., 2001b. Direction of gaze effects on early face processing: eyes-only versus full faces. Cogn. Brain Res. 10, 333–340.

Tipples, J., 2002. Eye gaze is not unique: automatic orienting in response to uninformative arrows. Psychon. Bull. Rev. 9, 314–318.

Van der Lubbe, R.H.J., Neggers, S.F.W., Verleger, R., Kenemans, J.L., 2006. Spatiotemporal overlap between brain activation related to saccade preparation and attentional orienting. Brain Res. 1072, 133–152.

Van Velzen, J., Eimer, M., 2003. Early posterior ERP components do not reflect the control of attentional shifts towards expected peripheral events. Psychophysiology 40, 827–831.

Von Grünau, M., Anston, C., 1995. The detection of gaze direction: a stare in-the-crowd effect. Perception 24, 1297–1313.

Vlamings, P.H.J.M., Stauder, J.E.A., van Son, I.A.M., Mottron, L., 2005. A typical visual orienting to gaze- and arrow-cues in adults with high functioning autism. J. Autism Dev. Disord. 35, 267–277.

Vuilleumier, P., 2002. Perceived gaze direction in faces and spatial attention: a study in patients with parietal damage and unilateral neglect. Neuropsychologia 40, 1013–1026.

Watanabe, S., Miki, K., Kakigi, R., 2002. Gaze direction affects face perception in humans. Neurosci. Lett. 325, 163–166.

Wicker, B., Michel, F., Henaff, M.-A., Decety, J., 1998. Brain regions involved in the perception of gaze: a PET study. Neuroimage 8, 221–227.

Wright, M.J., Geffen, G.M., Geffen, L.B., 1995. Event related potentials during covert orientation of visual attention: effects of cue validity and directionality. Biol. Psychol. 41, 183–202.

Yamaguchi, S., Tsuchiya, H., Kobayashi, S., 1994. Electroencephalographic activity associated with shifts of visuospatial attention. Brain 117, 553–562.