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RESEARCH****Research Report**

# Faster, more intense! The relation between electrophysiological reflections of attentional orienting, sensory gain control, and speed of responding

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## ABSTRACT

Selective visual attention is thought to facilitate goal-directed behavior by biasing the system in advance to favor certain stimuli over others, resulting in their selective processing. The aim of the present study was to gain more insight into the link between control processes that induce a spatial attention bias, target selection processes and speed of responding. To this end, participants performed a spatial cueing task while their brain activity was recorded using EEG. In this task, cues either validly or invalidly predicted the location (left or right) of a forthcoming imperative stimulus or provided no information regarding its location. Cues directing attention in space elicited greater positivity over fronto-central and contralateral posterior scalp regions than non-informative cues starting around 320 ms post cue. Targets appearing at attended vs. unattended locations evoked larger P1 and N1 components, indicating enhanced perceptual processing. Interestingly, detection of targets was fastest in trials with most cue-evoked posterior positivity and in trials with largest target-evoked N1 amplitude. Importantly, the greater the difference in cue-evoked posterior positivity between fast and slow trials, the greater the difference in target-evoked N1 amplitude between fast and slow trials was. Together these findings support neurobiological models of attention that postulate that preparatory attention to a particular location in space can bias the system in advance to favor stimuli presented at the attended location, resulting in a modulation of perceptual processing of incoming stimuli and facilitated goal-directed behavior.

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## 1. Introduction

In order to deal with the wealth of sensory input surrounding us, the human mind is equipped with a selection mechanism that is known as attention. Attention can be dynamically allocated in advance to locations in the visual field, where goal-relevant information is likely to appear. This allows the observer to selectively process information from this location

when it appears and to respond faster and more accurately to behaviorally important events (e.g., Posner, 1980). Recent electrophysiological and neuroimaging studies in humans, as well as single unit recordings in animals have demonstrated that attention can bias information processing in a top-down manner by increasing the sensitivity of neurons that are responsive to relevant stimulus features and by decreasing the sensitivity of neurons responsive to irrelevant stimulus

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features (Motter, 1993). Recent functional neuroimaging studies have shown that this top-down bias is generated by a fronto-parietal network of brain areas involved in orienting and maintaining the focus of attention (Brunia, 1999; Hopfinger et al., 2000, 2001) and expressed in perceptual areas of the brain, including extra-striate visual cortex. For example, several studies have shown enhanced preparatory activation in visual areas that code the attended location in the absence of any stimulation (Giesbrecht et al., 2006; Hopfinger et al., 2000; Kastner et al., 1999; Woldorff et al., 2004).

A common paradigm used for studying the effects of advance preparation on stimulus processing and behavior is the symbolic spatial cueing task, developed by Posner and co-workers (Posner, 1980; Posner and Cohen, 1984). In this task, participants are required to respond to an imperative stimulus that is presented randomly in either the left or right visual hemifield. Importantly, prior to this stimulus, a symbolic cue is presented providing information concerning the likelihood of the location of the imperative stimulus. Participants can take advantage of this information by covertly shifting their attention (i.e., without moving their eyes) to the cued location in preparation for the presentation of the target stimulus. Behavioral studies have shown that participants are typically faster and more accurate (Posner, 1980; Posner and Cohen, 1984; Posner and Petersen, 1990) at responding to imperative stimuli presented at the cued location (valid cue) compared to imperative stimuli presented at the opposite or uncued location (invalid cue). In addition to left and right attention-directing cues, many behavioral studies have included a “neutral” or non-informative cue condition, in which the cue does not provide any information about the location of the forthcoming imperative stimulus. Response times to imperative stimuli preceded by non-informative cues are typically intermediate to those preceded by valid or invalid cues.

In recent years, several studies have used the event-related potential (ERP) technique to directly measure cue-triggered attentional orienting processes whose existence in behavioral paradigms is typically inferred only by the indirect measure of performance on target stimuli. To isolate attention shift-related processes, many of these ERP studies directly contrasted ERPs elicited by left and right attentional directing cues. Using this contrast, three principal attention shift-related ERP effects have been identified, which generally are more pronounced over the hemisphere contralateral to the location indicated by the cue. The first of these effects consists of an early directing attention negativity (EDAN) that is maximal over contralateral posterior scalp locations between 200 to 400 ms post cue (Harter et al., 1989; Harter and Anllo-Vento, 1991; Hopf and Mangun, 2000). This negativity appears to shift to more fronto-central scalp locations slightly later in time, between 300 and 500 ms, resulting in a second component, the anterior directing attention negativity (ADAN) (Eimer et al., 2002; Nobre et al., 2000). These two ERP components have been hypothesized to reflect the interpretation of the cue as to the aspect of expected locations and the consecutive shift of attention to this location, respectively. In particular, the EDAN has been thought to reflect a more or less reflective orienting of attention to the location where the relevant cue information is presented (van Velzen and Eimer, 2003). In this respect, the EDAN bears some similarities with the N2pc component (Luck

and Hillyard, 1994), which is believed to reflect the deployment of attention to a relevant stimulus location. The ADAN has been hypothesized to reflect some frontal control signal to shift attention. Two recent studies (Green and McDonald, 2006; Green et al., 2005), however, have suggested that the ADAN is not necessarily reflecting a generic attentional control mechanism, but is more specific to the visual domain. The EDAN and ADAN are sometimes followed in time by a late directing attention positivity (LDAP), that is maximal over posterior sites contralateral to the cued location (Eimer et al., 2002; Harter and Anllo-Vento, 1991; Mangun, 1994). The LDAP is thought to reflect the excitability of perceptual neurons that represent the cued location.

It has been argued that these lateralized shift-related components may not reflect the full temporal pattern of spatial orienting (Slagter et al., 2005a; Talsma et al., 2005). A comparison of ERPs elicited by attention-directing cues, regardless of which location they are indicating, with ERPs elicited by non-informative cues permits isolation of all attentional orienting processes that may be mandatory for the establishment of an attentional bias, including processes that are not lateralized. Using this approach, we found a relatively early broadly distributed positive ERP deflection that was elicited by the attention-directing cues, which started before the onset of the EDAN, at around 160 ms after cue onset (Talsma et al., 2005). This component was interpreted as reflecting the initiation of a shift of attention and was followed by a negatively shifted potential over central scalp regions, starting at around 400 ms after cue onset, that was interpreted as reflecting the establishment of a general state of preparation. In addition, two other recent studies have reported parietal positivities to cues directing attention to a single task-relevant stimulus feature in comparison to non-informative cues (Slagter et al., 2005a) or cues that repeatedly directed attention to the same stimulus feature (Slagter et al., 2005b). Slagter et al. refined the interpretation of this shift-related positivity in terms of a translation of cue-symbol information into an actual shift of attention.

Taken together, these findings can be interpreted as reflecting a sequence of events, in which the EDAN or N2pc reflects a more or less automatic selection of the relevant cue feature, which is then followed by a translation of the cue (posterior positivity) into a shift of attention (late negativity).

Next to these attentional orienting-related effects, ERP studies have examined the effect of attention on brain responses related to stimulus processing. They have generally shown that the amplitude of two early stimulus-evoked components, known as the P1 (~80 ms after stimulus onset) and the N1 (~180 ms after stimulus), is enhanced for attended compared to unattended stimuli (see Hillyard et al., 1998 for a review). Although these modulations of P1 and N1 amplitudes were initially interpreted as a unitary “sensory gain” effect, it is currently believed that the P1 and N1 components reflect two qualitatively different mechanisms (Luck et al., 1994; Mangun, 1994; Talsma et al., 2005). It was found that the stimulus-evoked P1 amplitude was reduced in invalidly cued trials compared to validly and non-informatively cued trials. In contrast, the N1 amplitude was enhanced in validly cued trials compared to invalidly and non-informatively cued trials. This seems to suggest that while P1 amplitude may reflect the

suppression of information from irrelevant locations in the visual field, N1 amplitude may be specifically related to the gain control of relevant stimuli.

The above described findings support neurocognitive models of selective visual attention that postulate that preparatory attention to a particular location in space can bias the system in advance to favor stimuli presented at the attended location, resulting in a modulation of perceptual processing of incoming stimuli and improved task performance (e.g., Desimone and Duncan, 1995; LaBerge, 1995, Mangun and Hillyard, 1988). According to such models, one would expect that varieties in reaction times could be largely attributed to varieties in the strength of the attentional focus. That being the case, one would expect that the amplitude of the abovementioned components (i.e., the shift-related positivity and/or the biasing negativity), would vary in amplitude as a function of response time.

At present, only few studies have directly examined the relationship between cue-triggered orienting processes, subsequent attentional modulations of stimulus processing, and performance measures (Jongen et al., 2006; Schröger and Eimer, 1997). Jongen et al. addressed this question in part by investigating how ERP components related to non-specific preparation changed as a function of response time. They found that fast responses were associated with increases in contingent negative variation (CNV; Walter et al., 1964) activity, and decreases in alpha band power in the interval between non-informative cue and imperative stimulus. Jongen et al. focused on examining nonspecific preparation processes only, however, without addressing the effects of selective location-specific preparation on response time. Another recent study (Thut et al., 2006) investigated the relation between the strength of the spatial attention bias, as indexed by alpha activity over occipital cortex, and speed of responding. Lower alpha power over occipital scalp regions contralateral to the cued location was associated with faster response times to forthcoming target stimuli. This study shows that the strength of the attentional bias can influence the speed of target processing, but did not examine the relation between control processes responsible for generating this attentional bias and subsequent target processing.

The aim of the present study was to examine the relation between attentional orienting, gain control, and response times, by taking advantage of trial-by-trial variations in response times during performance of a symbolic spatial cueing task. In our symbolic cueing task, an imperative stimulus was presented in the left or the right visual hemifield within 800 to 1800 ms after a valid or invalid attention-directing cue or after a non-informative cue. While participants performed this task, their electroencephalogram was recorded using 64 electrodes. We expected to replicate the classical behavioral and electrophysiological patterns of results, summarized above. In addition, the present study investigated the relation between attentional orienting, gain control, and response times, by classifying each trial as 'fast', 'somewhat fast', 'somewhat slow', or 'slow' based upon the participant's response time. The underlying assumption was that there are natural trial-to-trial fluctuations in the strength of the attentional focus, which influence the way stimuli are processed in the brain and subsequent task performance. More

specifically, on some trials attention is better focused than on other trials, resulting in faster response times to target stimuli. We had three main predictions. Firstly, we expected the strength of processes involved in generating and/or maintaining the biased attentional state to be related to the speed of target processing. In particular, we predicted that the shift-related positivities (Slagter et al., 2005a,b; Talsma et al., 2005) and the slow negative wave following this positivity (Talsma et al., 2005) would both be correlated with RTs. We used a cue-symbol that was symmetrical and physically identical across conditions; however, the relevant cue information was always located ipsilaterally with respect to the cued location. Some authors have argued that such a cue design triggers an automatic reflective orienting of attention to the location of this relevant cue feature, presumably resulting in an N2pc component (i.e., van Velzen and Eimer, 2003). Since this process is presumed to be a more or less exogenous pull of attention, we did not expect the amplitude of such a potential N2pc component to vary with the variations in the voluntary control of attentional orienting to the cue, and hence to correlate with response time. Secondly, we expected to find differences in the amplitude and/or latency of imperative stimulus-evoked ERP components between fast and slow validly cued trials. In particular, we expected to observe greater N1 amplitudes in fast vs. slow trials, since this component has been shown to be enhanced by attention (cf. Luck et al., 1994; Mangun, 1994; Talsma et al., 2005). Thirdly and lastly, we expected those individuals that showed the greatest difference in orienting processes between fast and slow trials to show the greatest difference in target modulation between fast and slow trials.

## 2. Results

### 2.1. Behavior

#### 2.1.1. Response times

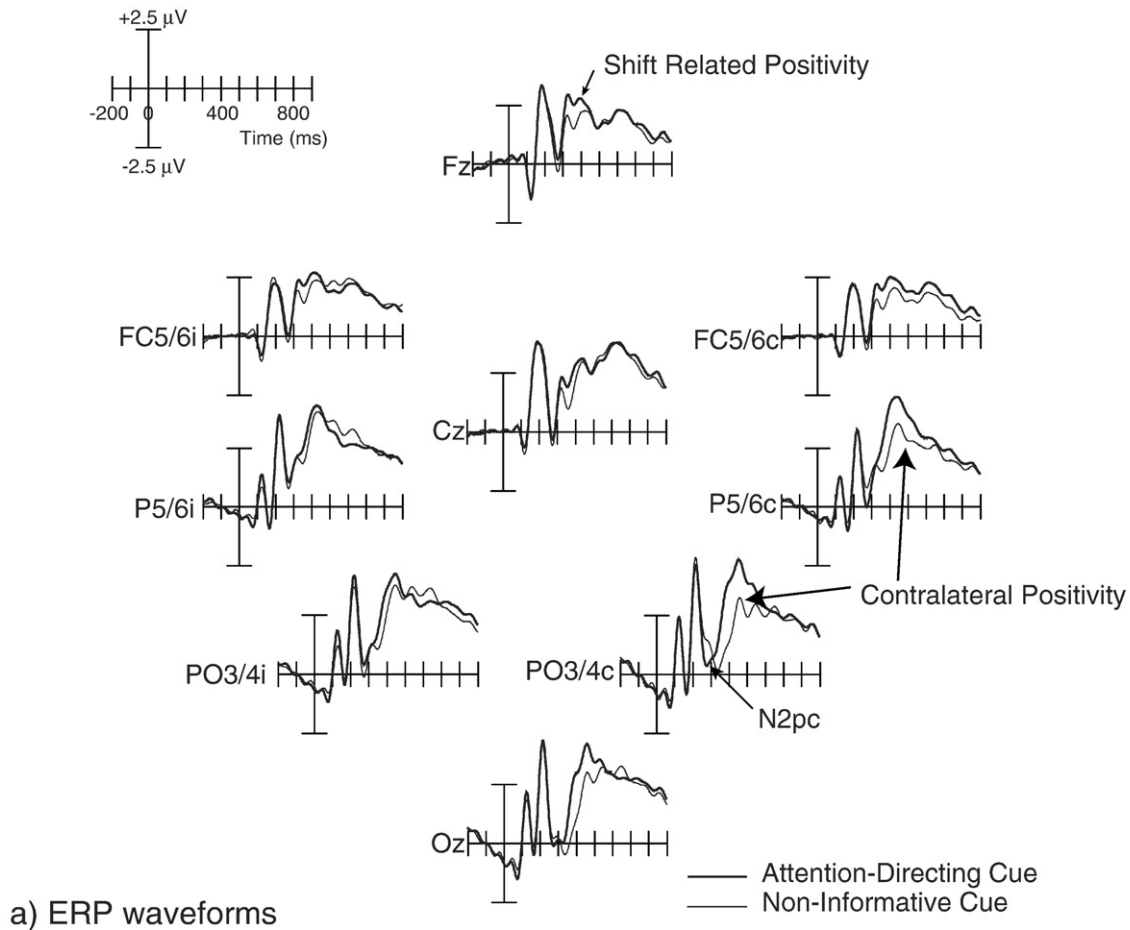
See Table 1 for response times in the different cue conditions (valid, invalid, non-informative). As expected, replicating previous findings, participants were significantly fastest in detecting validly cued targets and slowest in detecting invalidly cued targets, as reflected in a highly significant main effect of Cue Validity ( $F(2,24)=71.8; p<.0001; \epsilon=.64$ ). Post hoc comparisons showed that response times to invalidly cued targets were significantly longer than non-informatively cued targets ( $F(1,12)=55.0; p<.0001$ ). Response time to non-informatively cued targets, in turn, was also significantly longer than those to validly cued targets ( $F(1,12)=49.5; p<.0001$ ). Responses

**Table 1 – Mean response times and accuracies**

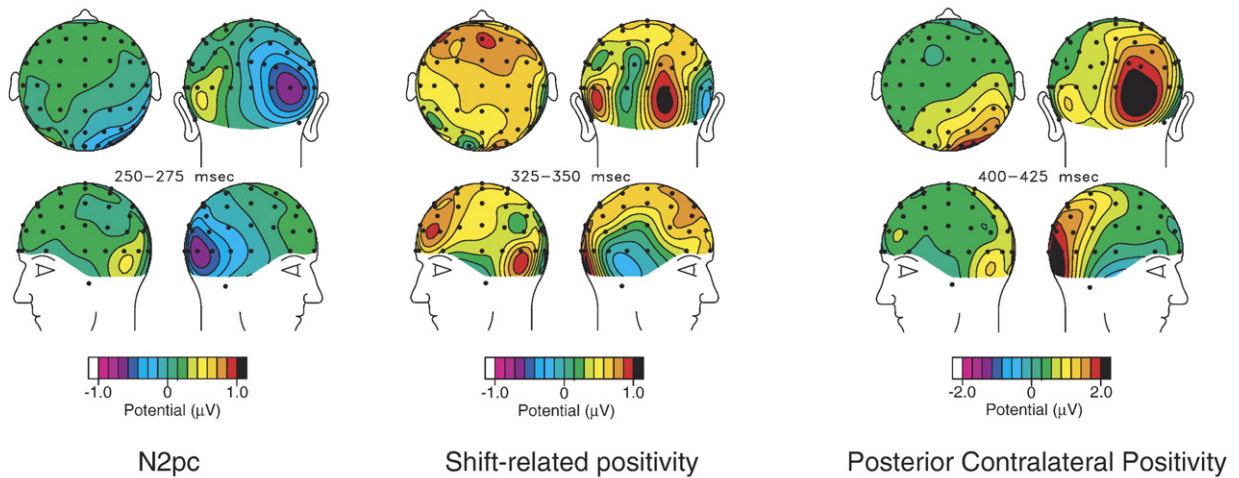
	Cue validity		
	Valid	Non-informative	Invalid
Response time	462 (14.3)	486 (14.9)	535 (12.6)
Accuracy	94.5 (.9)	91.0 (1.3)	87.9 (1.7)

Note. Response times are in ms, accuracies are in percentage correct. Standard error is given in parentheses.

Cuing Effects



a) ERP waveforms



b) Scalp topographies

**Fig. 1 – ERP data in the cue–target interval. Panel a shows the ERP waveforms elicited by attention-directing and non-informative cues. The main sequence of attention-directing brain processes consists of an initial contralateral N2 (N2pc) effect, which is followed by a fronto-centrally distributed shift-related positivity. The shift-related positivity is then followed by a large posterior positivity, which has a contralateral occipital scalp maximum. Panel b shows the scalp distribution of the effects of interest.**

to the validly cued trials were subsequently separated into four quartiles yielding the following response times First quartile: mean RT=363 ms (SD=57 ms); second quartile mean RT=392 ms (SD=65 ms); third quartile mean RT=420 ms (SD=78 ms); fourth quartile mean=600 ms (SD=150 ms).

### 2.1.2. Accuracy

Further replicating prior findings, accuracy rates were highest for validly cued targets and lowest for invalidly cued targets (see Table 1), as reflected by a significant main effects of Cue Validity ( $F(2,24)=15.9$ ;  $p<.0001$ ;  $\epsilon=.89$ ). Post hoc comparisons revealed that responses to invalidly cued targets were less accurate than targets preceded by a non-informative cue ( $F(1,12)=8.16$ ;  $p<.01$ ). Similarly, non-informatively cued targets were less accurate than validly cued targets ( $F(1,12)=11.0$ ;  $p<.01$ ).

## 2.2. Electrophysiological data: cue-locked ERPs

### 2.2.1. ERPs related to attentional orienting

Fig. 1 shows the ERPs elicited by attention-directing cues contrasted with ERPs evoked by non-informative cues. As can be seen in this figure, there were several notable differences in

scalp-recorded brain activity between attention-directing and non-informative cues over contralateral posterior scalp regions. These differences were tested by computing mean amplitudes of consecutive 20 ms windows from electrodes (P1/2i, Pz, P1/2c, PO1/2i, POz, PO1/2c, O1/2i, Oz, and O1/2c) and subjecting these values to separate within-subjects ANOVAs with the factors Cue Type (Attention-directing vs. Non-informative), Area (Frontal, Central and Parietal electrodes), and Laterality (Ipsilateral, Central, and Contralateral). These analyses showed that attention-directing cues elicited significantly greater negativity than non-informative cues over posterior electrode sites contralateral to the cued location (see for example the P03/4c recording sites) in the time window of the N2, between 240 and 280 ms after cue onset. This early contralateral effect was reflected by an interaction between Cue Type and Laterality ( $F_s(2,24)=10.77$ – $11.13$ ;  $p<.05$ ); and by a three-way interaction between Cue Type, Area, and Laterality ( $F_s(4,48)=4.40$ – $8.09$ ;  $p_s<.05$ ).

Following this early contralateral negativity, attention-directing cues elicited greater positivity over posterior scalp regions than non-informative cues. This difference in positivity was reflected by a significant main effect of Cue Type ( $F_s(1,12)=8.14$ – $28.06$ ;  $p_s<.05$ – $.0005$ ), between 360 and 440 ms.

## Effects of Response Speed on Valid Attention-Directing Cues

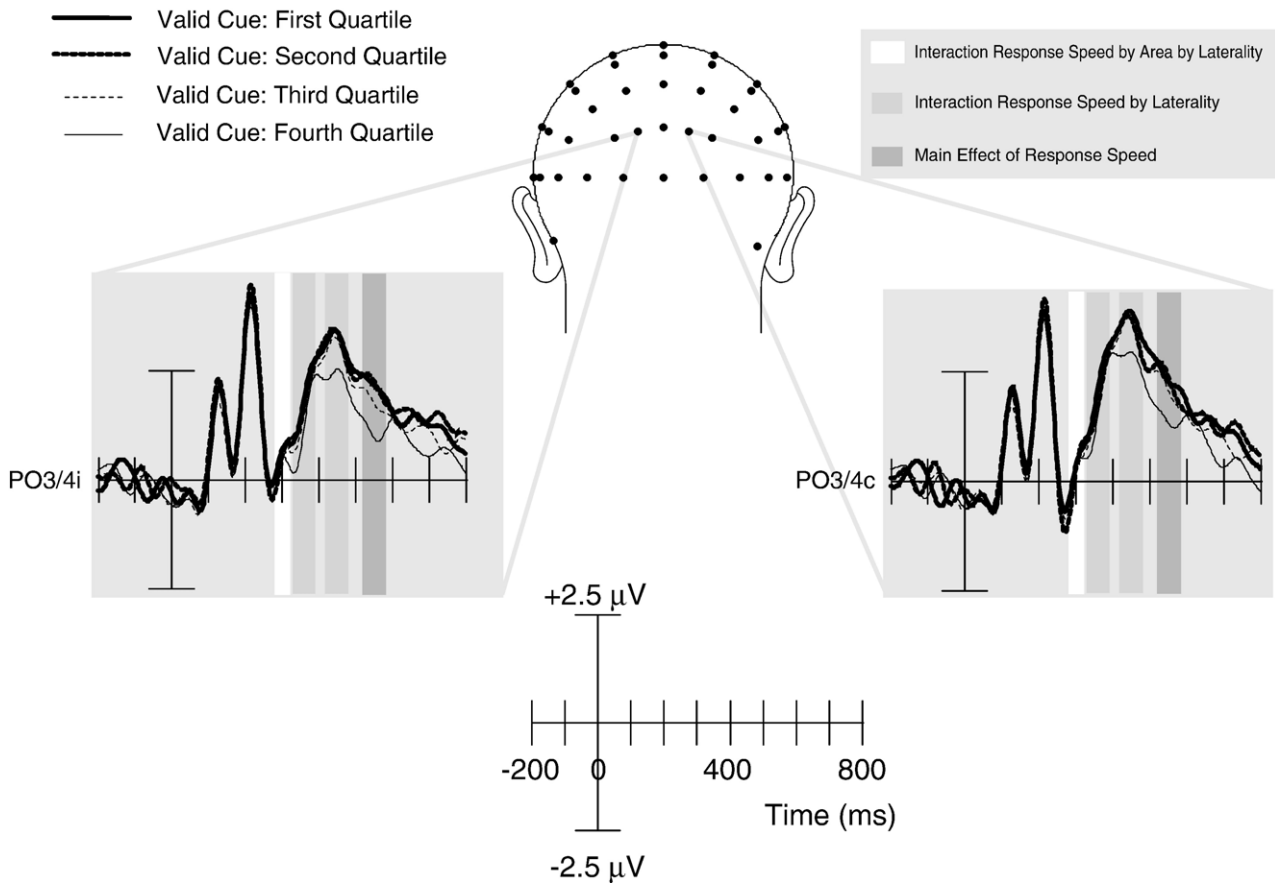


Fig. 2 – Effects of response time on cue-evoked ERPs, as shown on a bilateral occipital electrode pair. Grey bars indicate the latency ranges in which the amplitudes of the shift-related ERP components interacted with the response speed to the subsequent target stimulus.

This effect was significantly larger over the hemisphere contralateral to the cued location, specifically at occipital and parieto-occipital sites, as can be seen in Fig. 1B (significant interaction between Cue Type and Laterality between 360 and 640 ms after cue onset;  $F_s(2,24)=5.02\text{--}10.8$ ;  $ps<.05\text{--}.01$ ).

Next to these contralateral posterior effects, several more broadly distributed effects of Cue Type were observed using repeated measures ANOVAs that included electrodes F3/4i, Fz, F3/4c, C3/4i, Cz, C3/4c, P3/4i, and P3/4c. First, starting around 320 ms after cue onset, ERPs elicited by attention-directing cues were positively displaced relative to those elicited by non-informative cues, as indicated by a significant main effect of Cue Type between 320 and 420 ms after cue onset ( $F_s(1,12)=5.47\text{--}12.4$ ,  $ps<.05\text{--}.01$ ). This broadly distributed effect appeared strongest over contralateral dorsal posterior sites, as reflected by significant interactions between Cue Type and Area (280–340 ms:  $F_s(2,24)=8.65\text{--}11.9$ ;  $ps<.01$ ; 380–440 ms:  $F_s(2,24)=7.02\text{--}4.74$ ;  $ps<.05$ ), between Cue Type and Laterality (480–640 ms:  $F_s(2,24)=6.61\text{--}10.50$ ;  $ps<.05\text{--}.005$ ) and between Cue Type, Area, and Laterality (360–420 ms:  $F_s(4,48)=4.61\text{--}4.98$ ;  $ps<.05$ ). In contrast to our previous study (Talsma et al., 2005), we did not find a sustained negativity in the longer latency (i.e., >400 ms post cue) cue–target interval.

### 2.2.2. Relation between response time and cue-locked ERPs

We next examined the relationship between cue-triggered processes and speed of responding. Fig. 2 shows the ERP traces of attention-directing cues that correctly predicted the target location separately for each response time quartile. Effects of response time on cue-related processes were analyzed by computing mean voltages of consecutive 20 ms time windows on electrodes P1/2i, Pz, P1/2c, PO1/2i, POz, PO1/2c, O1/2i, Oz, and O1/2c, and subjecting these to a within-subjects ANOVA with the factors Quartile (first to fourth, in order of increasing response time), Laterality (Ipsilateral, Midline, Contralateral), and Area (Parietal, Occipito-Parietal, and Occipital). As can be seen in Fig. 2, valid cues that were followed by slow responses elicited less positivity in particular over contralateral posterior scalp regions than valid cues that were followed by somewhat slow, somewhat fast, or fast responses. This difference in cue-triggered positivity between the different trial types was expressed in three statistical effects. First, the three-way interaction between Quartile, Area, and Laterality was significant between 240 and 320 ms after cue onset (Fig. 2,  $F_s(3,36)>3.05$ ;  $ps<.05$ ). Secondly, a significant interaction between Quartile and Area was found between 340 and 380 ms ( $F_s(3,36)>2.44$ ;  $ps<.05$ ) and between 420 and 460 ms after cue onset ( $F_s(3,36)>2.42$ ;  $ps<.05$ ). Thirdly, an overall effect of Response Speed was significant between 520 and 560 ms after cue onset ( $F_s(3,36)>3.08$ ;  $ps<.05$ ). Since Fig. 2 suggested that the ERP waves elicited by the slowest responses were of lower amplitude than those in the other three quartiles, 3 additional pair-wise comparisons were conducted in which the ERPs composed of the slowest trials were compared to each of the other ERPs. Again, this test was done using consecutive 20 ms time windows, again using the factors Quartile, Area, and Laterality. These tests showed that particularly at longer latencies (i.e., the 520 to 560 ms window) cues that were followed by relatively fast responses elicited greater positivity than cues followed by relatively slow

responses (i.e., first Quartile vs. fourth Quartile; significant between 480 and 540 ms; all  $F_s(1,12)>5.0$ ;  $ps<.05$ ; second Quartile vs. fourth Quartile; significant between 500 and 540 ms;  $F_s>5.0$ ;  $ps<.05$ ).

## 2.3. Electrophysiological data: target-locked ERPs

### 2.3.1. Attentional modulation of target-locked ERPs

ERP responses elicited by target stimuli are presented in Fig. 3. Effects of Cue Validity on the amplitude of the P1, N1, P2, N2, and P3 ERP components were examined using peak values measured at posterior electrodes P1/2i, Pz, P1/2c, PO1/2i, POz, PO1/2c, O1/2i, Oz, and O1/2c. These mean values were subjected to separate within-subjects ANOVAs containing the factors Cue Validity (Valid, Non-Informative, or Invalid), Area (Parietal, Parieto-Occipital, or Occipital), and Laterality (Ipsilateral, Central, Contralateral).

P1 amplitude was determined as the mean amplitude between 90 and 110 ms after stimulus onset. The amplitude of the P1 component was significantly affected by Cue Validity ( $F(2,24)=3.44$ ;  $p<.05$ ;  $\epsilon=.79$ ). In line with previous findings from ERP studies (Luck et al., 1994; Mangun, 1994; Talsma et al., 2005), planned comparisons showed that the amplitude of the P1 component was significantly smaller for invalidly cued targets compared to both validly cued targets ( $F(1,12)=5.42$ ;  $p<.05$ ) and non-informatively cued targets ( $F(1,12)=8.95$ ;  $p<.05$ ). The P1 components elicited by validly and non-informatively cued targets did not differ significantly from each other, however, ( $F<1$ ).

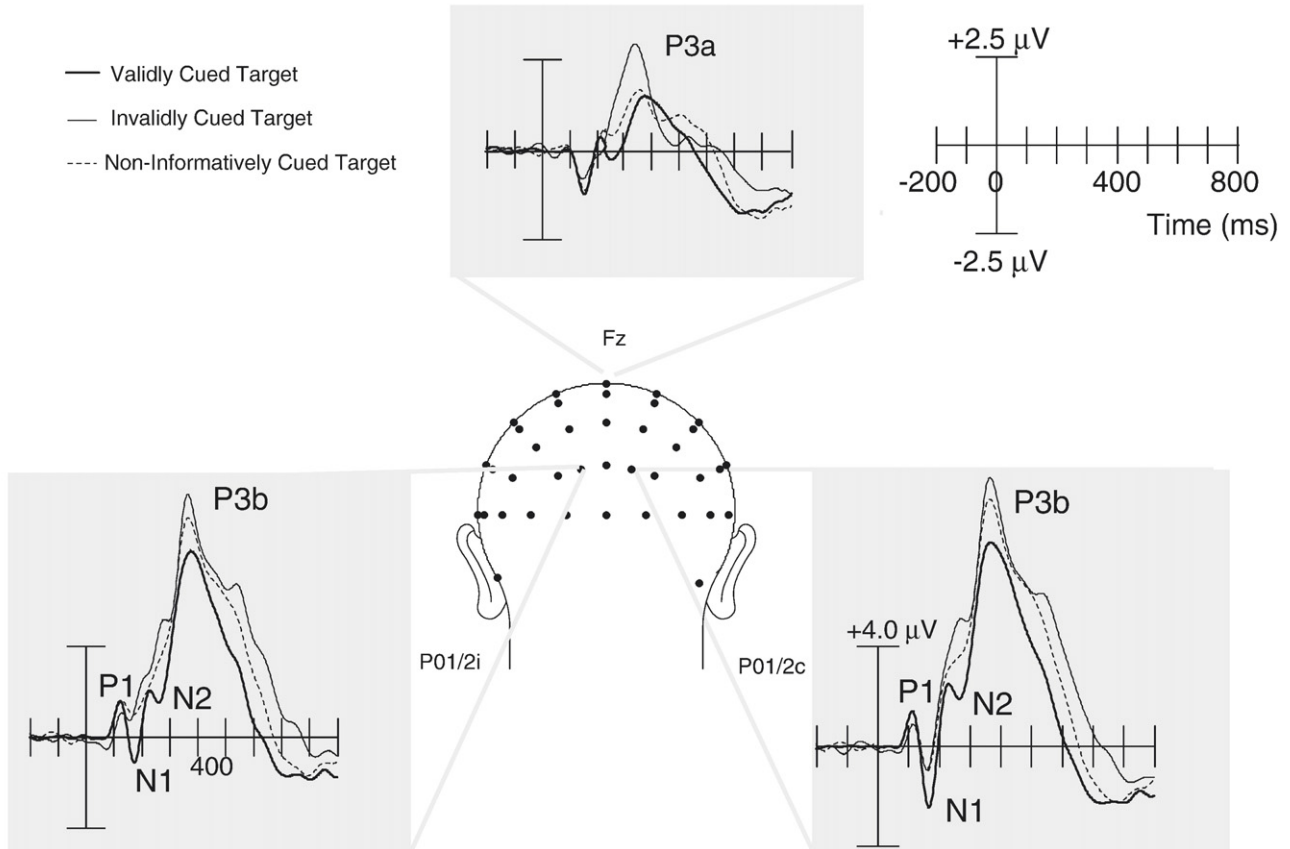
The amplitude of the N1 was determined as the mean amplitude between 140 and 200 ms after target onset. Further replicating previous findings (Luck et al., 1994; Mangun, 1994; Talsma et al., 2005), the amplitude of this component was significantly affected by Cue Validity ( $F(2,24)=9.51$ ;  $p<.01$ ;  $\epsilon=.70$ ), but revealed a somewhat different pattern of results than that for the P1. Here, the amplitude of the N1 was larger for validly cued targets compared to both non-informatively cued targets ( $F(1,12)=12.77$ ;  $p<.005$ ), and invalidly cued targets ( $F(1,12)=9.82$ ;  $p<.01$ ). The N1 amplitude elicited by the latter two target types (non-informatively cued targets and invalidly cued targets) did not differ significantly from each other ( $F<1$ ).

In addition to these early attention-related P1 and N1 amplitude modulations, two additional effects of cue validity were observed. First, between 220 and 300 ms after target onset, a highly significant posterior N2 effect was found ( $F(2,24)=15.13$ ;  $p<.005$ ;  $\epsilon=.64$ ). Post hoc tests showed that the N2 amplitude differed significantly in all three Cue Validity conditions (all comparisons ( $F(1,12)>6.15$ ;  $p<.02$ ). Secondly, the amplitude of the P3 was affected by Cue Validity ( $F(2,24)=9.15$ ;  $p<.001$ ;  $\epsilon=.70$ ); P3 amplitude was largest on invalidly cued targets and smallest on validly cued targets.

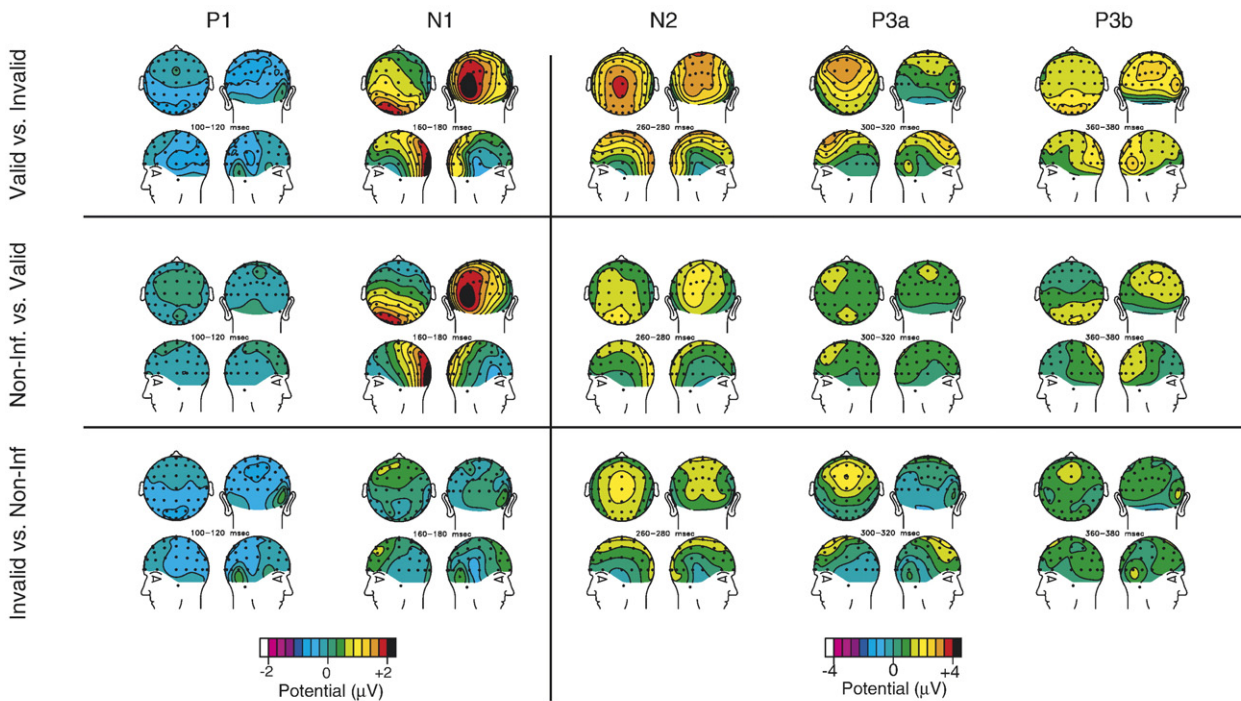
### 2.3.2. Relation between response time and target-locked ERPs

We next examined the relationship between these target-evoked processes and response times. Fig. 4 shows the ERPs elicited by validly cued targets, separately for fast, somewhat fast, somewhat slow, and slow response trials. Effects of response time were analyzed by determining the peak amplitude of each ERP component on electrodes P1/2i, Pz, P1/2c, PO1/2i, POz, PO1/2c, O1/2i, Oz, and O1/2c, and subjecting these values

### Cue Validity Effects on Target ERPs

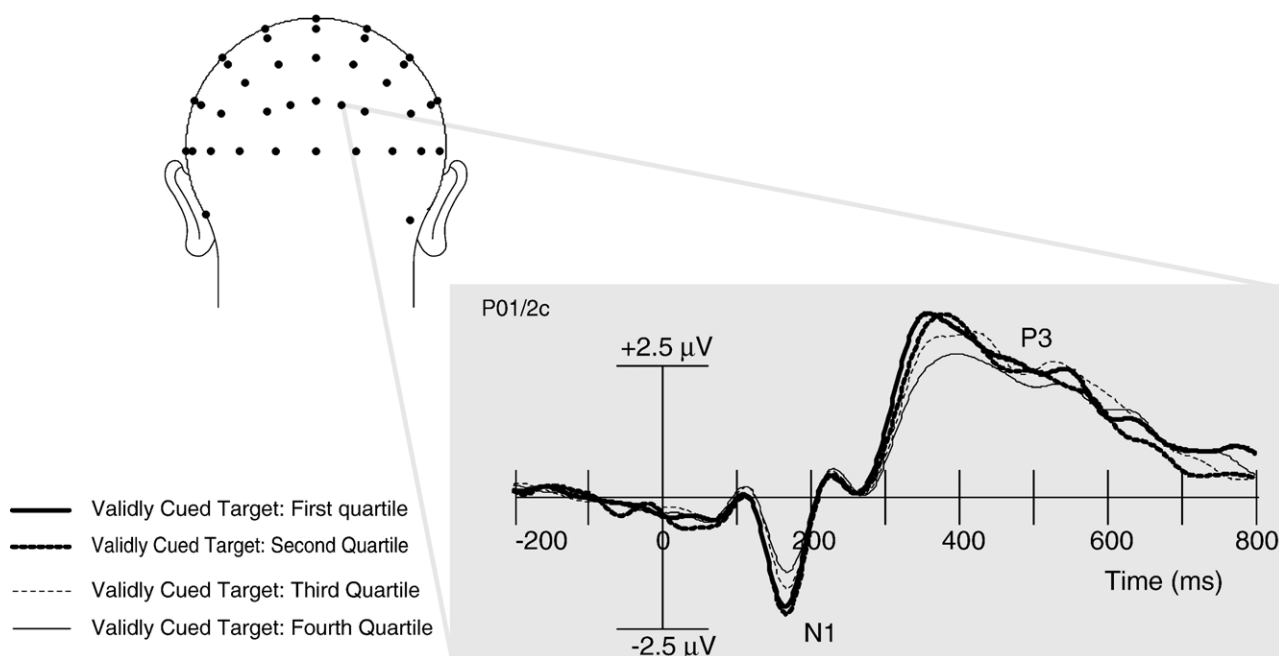


a) ERP Waveforms



b) Scalp Topographies

## Effects of Response Speed on ERPs Elicited by Target Stimuli



**Fig. 4** – Effects of response time on target-evoked ERPs, illustrated on one contralateral occipital electrode. Notice that the N1 component was significantly related to the response time on each trial. The faster the responses were, the larger the N1 amplitude was.

to a within-subjects ANOVA with the factors Quartile (first to fourth, in order of increasing response time), Laterality (Ipsilateral, Midline, Contralateral), and Area (Parietal, Occipito-Parietal, and Occipital). As can be seen in Fig. 4, trials with slow responses were characterized by a relatively small N1, while trials with fast responses were characterized by a relatively big N1. This difference in N1 amplitude was signified as a main effect of Quartile ( $F(3,36)=11.85$ ;  $p<.0001$ ;  $\epsilon=.073$ ). Planned comparisons showed that the N1 amplitude significantly increased from the fourth to the third quartile ( $F(1,12)=5.00$ ;  $p<.05$ ). Similarly, the N1 amplitude further increased from the third to the second quartile ( $F(1,12)=35.05$ ;  $p<.005$ ). No significant difference in N1 amplitude could be found between the first and second quartile ( $F(1,12)<1$ ), however. Interestingly, the N1 amplitude correlated strongly with the 520–560 ms RT difference effect in the cue-evoked effect as was shown by a significant correlation between these two effects ( $r=.56$ ;  $t(11)=2.26$ ;  $p<.05$ ). The N1 component peaked on average at 162 ms after stimulus onset. The latency of the N1 component was not affected by response time: ( $F<1$ ).

In addition to this effect of N1 amplitude on speed of responding, we also found, as expected, that the amplitude of the P300 was associated with the speed of responding. This asso-

ciation was analyzed by computing mean amplitudes of consecutive 20 ms time windows from electrodes P1, Pz, P2, PO1, POz, PO2, O1, Oz, and O2. These mean voltages were subjected to separate repeated measures ANOVA, with Quartile (four levels, corresponding with increasing response times), Laterality (3 levels: Ipsilateral, Midline, and Contralateral), and Area (3 levels: Parietal, Occipito-Parietal, and Occipital) as within-subjects factors. These analyses revealed a main effect of Quartile between 280 and 400 ms after stimulus onset ( $F(3,36)=4.06$ ;  $p<.05$ ). Planned comparisons showed that the P3 amplitude was significantly smaller on fast (fourth quartile) response trials compared to third quartile trials ( $F(1,12)=11.78$ ;  $p<.005$ ). No significant P3 amplitude differences were found between third and second quartile trials ( $F<1$ ) or second and first quartile trials ( $F<1$ ). Finally, although Fig. 4 suggests that the P3 peak latency varied somewhat with between quartiles, this was not significant ( $F(3,36)=1.60$ ;  $p=.2$ ).

### 3. Discussion

The aim of the present study was to investigate the relation between the physiological indices of attentional orienting and

**Fig. 3** – ERPs elicited by the target stimuli. Panel a shows the ERP wave forms on two occipital and one frontal channel. Occipital effects consist of a sequence of P1, N1, P2, N2, and P3b components. The P1 was specifically reduced in amplitude on invalidly cued targets, whereas the N1 was specifically enlarged on validly cued targets. Frontal channels show a small P3a component elicited by the (infrequent) invalidly cued targets. Panel b shows the scalp topography of the difference between each condition on each of the components of interest.

the speed of responding. This was done by categorizing trials in a symbolic cueing paradigm according to response time to a target stimulus. ERPs that were elicited by attention-directing symbolic cues preceding each target were compared on the basis of the response time to this target. ERPs elicited by the targets were categorized on the basis of response time in the same way. Results showed that ERPs elicited by cues and targets alike were affected by response time, demonstrating that trial-by-trial variations in response time can to a substantial degree be explained by variations in the effectiveness of attentional allocation. This novel finding is in line with neurocognitive models of selective visual attention that postulate that preparatory attention to a particular location in space can bias the system in advance to favor stimuli presented at that location, resulting in a modulation of perceptual processing of incoming stimuli and improved task performance (e.g., Desimone and Duncan, 1995; Mangun and Hillyard, 1988). In addition, the present study investigated the electrophysiological signatures of attentional orienting in more depth by comparing attention-directing cue conditions with a non-informative baseline. The main results from this study will be discussed below.

### 3.1. Cue-locked ERPs

Directing attention to locations was associated with enhanced negativity over contralateral posterior scalp regions between 240 and 280 ms post cue, which was followed in time by a fronto-centrally distributed positivity, starting at 320 ms, and enhanced positivity over contralateral posterior scalp areas, starting at 360 ms post cue. The early contralateral negativity likely reflects processes involved in selecting the task-relevant part of the cue-symbol. Previous studies using cues of which the task-relevant part is lateralized with respect to fixation (e.g., Nobre et al., 2000; van Velzen and Eimer, 2003) have shown that the deployment of attention to this part of the cue (i.e., slightly to the left or right of fixation) is reflected in a posterior contralateral negativity, also referred to as the N2pc. This component is believed to be indicative of the deployment of attention (Eimer, 1996, 1998; Hickey et al., 2006; Hopf et al., 2000, 2004; Luck and Hillyard, 1994; Wijers et al., 1997). In the present data, a similar N2pc could be observed in response to attention-directing cues between 240 and 280 ms post cue, suggesting that this first orienting-related effect likely represents the deployment of attention to that point of the star symbol cue that possessed the relevant (i.e., attention-directing) color.

This contralateral negativity was followed slightly later in time by a fronto-centrally distributed orienting-related positivity at about 300 ms after cue onset. This broadly distributed positivity presumably reflects the activation of the fronto-parietal attentional control network involved in orienting attention (Talsma et al., 2005). Note that this component started slightly later in the present study compared to in earlier studies by Mangun (1994) and Talsma et al. (2005), which also directly compared activity elicited by attention-directing and non-informative cues. In these studies, fronto-central effects were observed already at about 200 ms after cue onset. This is possibly due to the fact that these studies used arrow cues pointing to the left or right to

orient attention. It has been argued that arrow cues are over-learned symbols and as such provide relatively direct information regarding the to-be-attended location (Ristic et al., 2002; Tipples, 2002). This likely enables observers to more quickly orient attention in comparison to more symbolic cues.

This fronto-centrally distributed positivity was accompanied in time by a contralateral posterior positivity. The amplitude of this orienting-related positivity was linked to response times to the subsequently presented target stimulus, such that valid cues that were followed by targets eliciting relatively fast responses evoked greater posterior positivity than valid cues that were followed by targets eliciting relatively slow responses. This finding suggests that this orienting-related ERP component may reflect processes that are mandatory for the establishment of a spatial attentional bias and extends findings from previous behavioral and ERP studies of attentional orienting, which could not, or did not examine the relationship between preparatory processes and subsequent behavior in a cueing task. Several ERP studies have reported similar orienting-related posterior positivities. For example, Slagter et al. (2005a) found greater positivity to attention-directing compared to non-informative cues over lateral posterior electrode sites between 260 and 400 ms. This effect was localized to ventral posterior cortex and related to processes that translate the cue-symbol into an attention shift. It should be noted that this posterior positivity does not simply reflect cue-symbol interpretation processes (Woldorff et al., 2004), as the non-informative cue had to be semantically interpreted as well. In contrast to the current study, in the Slagter et al. (2005a) study, this posterior positivity was not lateralized with respect to the cued location. This may be related to the fact that symbolic letter cues, which were not asymmetric with respect to fixation, were used to orient attention. In our study, the relevant part of the cue was asymmetric with respect to fixation and this may have resulted in greater activation of contralateral occipital areas representing the cue-symbol. In this respect, it should also be noted that the late negative slow wave, observed in Talsma et al. (2005), was mostly absent in the present study. Differences between studies in experimental design, such as the specific cues used to direct attention or in the possible length of the cue–target interval (here: between 800 and 1800 ms; in Talsma et al., 2005: 200 and 800 ms), might explain this discrepancy. More research would be needed to fully address this issue, however.

It should be noted that the contralateral posterior positivity, in particular the later part of this effect, may alternatively reflect greater activation of areas of visual cortex that represent the cued location. Several studies have reported greater positivity over posterior scalp regions contralateral to the cued hemifield starting around 400 to 500 ms post cue (Eimer et al., 2002; Harter and Anllo-Vento, 1991; Hopf et al., 2000; Mangun, 1994). This contralateral positivity was assumed to reflect the modulation of the cortical excitability in regions, which are preparing to receive relevant visual information. A recent EEG study observed a cue-triggered decrease in alpha activity over occipital sites contralateral to the relevant location in space (Thut et al., 2006). The greater this decrease in alpha power in the cue–target interval was,

the faster responses were to a forthcoming target stimulus, suggesting a link between the momentary bias of visuospatial attention and imminent visual processing. The here observed association between contralateral posterior positivity and speed of responding may provide another index of this link.

Thus, attention seems to be set up by generic processes that are additional to cue-symbol interpretation processes and subserved by a fronto-parietal network of brain areas. These processes likely link the attention-directing cue to its associated test stimulus feature. The strength of the process by which the meaning of the cue is related to current goals and translated into a spatial attention bias may determine how well participants are prepared for the subsequent target task, as faster responses to target stimuli were associated with greater cue-related posterior positivity.

### 3.2. Target-locked ERPs

Target stimuli elicited the well-known sequence of P1, N1, P2, N2, and P3 components. The P1 was smaller on invalidly cued trials than on validly or non-informatively cued trials. In contrast, the N1 component was larger on validly cued trials than on non-informatively and invalidly cued trials. These results confirm that participants successfully shifted their attention in response to the attention-directing cues. In addition, these results replicate earlier observations that the P1 component is sensitive to the costs associated with invalid cues, whereas the N1 is predominantly sensitive to the benefits associated with valid cues (Luck et al., 1994; Mangun, 1994; Talsma et al., 2005).

As predicted, the better attention was focused in advance (as indexed by a larger target-evoked N1 amplitude), the faster response times were. This result implies a direct relation between neural sensitivity of perceptual brain areas and the efficiency with which a stimulus can be processed. Interestingly, the larger the difference in target-evoked N1 amplitude between fast and slow response trials was, the larger the difference in cue-evoked posterior positivity between fast and slow response trials was. This association between orienting-related processes and modulatory attention processes suggests that a less effective cue-symbol translation process may affect imminent target processing, leading to a delay in response.

It should be noted that this increase in N1 amplitude with faster responses argues against a possible alternative interpretation of the RT based ERP effects in the cue-target interval. One could argue that these effects were mainly caused by a subset of trials in which participants forgot to orient their attention. Although it is true that trials in which participants did not fully comply with task instruction could have contributed, we do not consider this to be the main contributing factor. If non-compliance with instruction was the main contributing factor, we would also have expected to find differences on the N1 amplitude between fourth quartile (i.e., slowest) trials and the other three quartiles. This was not the case, however, as the N1 amplitude in the third and fourth quartile trials did not differ from each other. Instead, we observed the most striking N1 effects on the faster trials.

### 3.3. Summary and conclusions

The present study investigated the link between processes that allocate attention in advance to locations in the visual field where a target stimulus is likely to appear, the subsequent processing of a target presented at this location, and the speed of responding to this behaviorally important event. We documented a posterior positivity that is modulated by covertly directing attention to a particular location in the absence of visual stimulation and is related to the processing speed of forthcoming targets at that location. In addition, enhanced attentional processing of target stimuli, as indexed by a larger target-evoked N1 amplitude, was linked to faster response times as well, providing evidence for a direct relation between gain control and response speed. Interestingly, the greater the difference in orienting-related posterior positivity between fast and slow trials, the greater the difference in target-evoked N1 amplitude between fast and slow trials was. This latter finding suggests a direct relationship between the strength of attentional preparation and modulatory effects of attention on subsequent target processing. Together these findings provide important support for models of attention that postulate that preparatory attention to a particular location in space can bias the system in advance to favor stimuli presented at that location, resulting in a modulation of perceptual processing of incoming stimuli and a faster response to target stimuli.

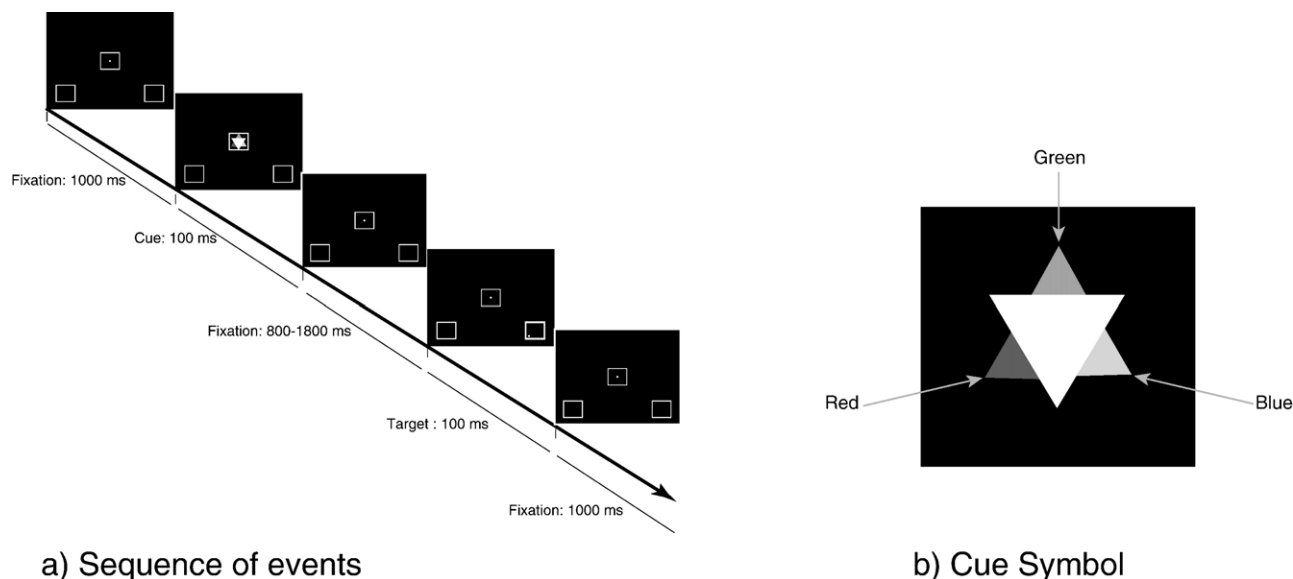
## 4. Experimental procedures

### 4.1. Participants

Sixteen volunteers (age 18–35, mean 22; 3 males) participated in the present study. All participants had normal or corrected-to-normal vision. None of them reported a history of mental or sustained physical illness. All participants gave informed consent prior to engaging in the experiment and received a financial compensation of 10 euros per hour. Three participants were excluded from the analyses, due to excessive noise in their EEG recordings.

### 4.2. Stimuli and task

Throughout the experiment, the locations of the cue and target stimulus were highlighted by means of a white outlined square (each location subtending a visual angle of 1.9° by 1.9°; see Fig. 5). Each trial started with the centrally presented fixation screen, which was presented with a duration of 1000 ms. This was followed by the presentation of a symbolic cue (duration 100 ms), presented inside the center rectangle, which informed participants about the most likely location (left or right lower hemifield) of a subsequently presented imperative stimulus. The cue-symbol consisted of a six-pointed star symbol (see Fig. 5), of which every alternate point was colored red, green, and blue, respectively. One point was always oriented to the lower left of the display, one always to the lower right of the display, and one point was always oriented upwards. The color of each point varied from



**Fig. 5 – (a) Outline of the paradigm. (b) Example of the symbolic cue used in the present study. Three points of a six-pointed star were uniquely colored. For each participant, only one of these colors was relevant. On each trial, the point with the relevant color was oriented toward either the lower left or lower right corners of the screen in case of a predictive cue. In addition, the relevant color could be pointing upward in case of a non-informative trial.**

trial to trial and participants were instructed to use the information indicated by the point of a predefined color to determine the most likely location at which the imperative stimulus could appear. For instance, when a participant was instructed that the red point of the cue was relevant, when this point was directed toward the lower left of the display (left attention-directing cue), the corresponding location was the most likely location at which the imperative stimulus could appear. Similarly, when the relevant (red, in case of our example) point was pointing to the lower right visual field (right attention-directing cue), this location was the most likely target location. Finally, when the relevant colored point was pointing upwards (non-informative cue), the location of the imperative stimulus could not be predicted. This particular cue design afforded the use of a physically identical cue in each condition, as each color was counterbalanced across participants. This cue was designed because pilot studies had shown that other forms of abstract cues, such as letters, yielded only a very small behavioral effect, which while reliably present, was deemed too small to base our RT based analyses on.

After a randomly variable SOA of 800 to 1800 ms, the imperative stimulus appeared, consisting of the transient (100 ms duration) thickening of the lines marking either the left or right imperative stimulus location (visual angles from center of box to fixation:  $4.8^\circ$  to the left or right of fixation, and  $4.8^\circ$  below fixation). The box was highlighted to create a transient visual luminance change that was needed to generate sufficiently large exogenous visual P1 and N1 components. Left and right hemifield imperative stimuli were presented with equal probability. Coinciding with this transients thickening of the lines, a gray dot was presented in either the lower-left or lower-right corner of the highlighted box. The relative location of this faint dot was also equiprobable.

Participants' task was to make a speeded button-press response to indicate the relative location of the faint dot stimulus within the highlighted box as fast as possible. They were required to report this location by pressing a response key with the index finger of the hand corresponding to the relative location of the dot. Following the response, a 1000 ms period followed during which time only the fixation dot and the location markers were presented, after which the next trial started. Participants performed a total of 960 trials. Two-third of all trials was predictive, and one-third was non-informative. Of the predictive trials, 75% was valid, and 25% was invalid. A total of 12 different target trials types were used, consisting of the factorial combination of Cue Instruction (Left, Right, or Non-Informative), Stimulus Location (Left or Right), and Target Dot Location (also Left or Right).

#### 4.3. Apparatus

Recordings took place in a sound attenuated, dimly lit, electrically shielded chamber. Participants sat in an adjustable chair, at a distance of approximately 120 cm in front of a 21-inch CRT computer screen. Stimulus presentation was controlled by a personal computer running the "E-Prime" software package (Psychology Software Tools Inc., Pittsburgh, PA, USA) and the Windows XP operating system. EEGs were recorded from 60 tin electrodes of the international 10–10 system, mounted in an elastic cap (Electro-Cap International Inc. Eaton, OH, USA) and referenced to the right mastoid during recording. Electrode impedances were kept below  $5\text{ k}\Omega$  for all electrodes. Horizontal eye movements were monitored by two electrodes at the outer canthi of the eyes. Vertical eye movements and eye blinks were detected by electrodes placed above and below the orbital ridge of the left eye. EEG was recorded using a .1 Hz high-pass filter, and a 100 Hz low-pass filter, using

a Neuroscan SynAmps (Compumedics USA Ltd., El Paso, TX, USA) acquisition system. Raw signals were continuously digitized with a sampling rate of 500 Hz, and a gain setting of 1000. Signals were digitally stored for off-line analysis.

#### 4.4. Procedure

Upon arrival, participants first received a brief explanation of the experimental procedures, filled out a consent form, and then practiced one block of 96 trials. Then, the EEG recording equipment was put in place, after which participants were allowed to briefly review their own online EEG recordings. During this review period, participants were also made aware of the consequences of movement and ocular artifacts on the EEG recording and received additional instructions to try and minimize these artifacts as much as possible. After this, the main experiment started, consisting of 10 blocks of 96 trials each. Each block of trials took about 5 min to complete.

#### 4.5. Data analysis

##### 4.5.1. Behavioral data

Mean response times and accuracy rates were computed separately for each participant and the three different cue types (valid, invalid, non-informative). These values were subjected to separate repeated measures analyses of variance (ANOVAs), containing the within-subjects factor Cue Validity (Valid, Non-Informative, or Invalid). Following this initial analysis, validly cued trials were subdivided into four quartiles, based on response time (first quartile: 25% fastest responses; second quartile: 25% to 50% fastest responses; third quartile: 50% to 25% slowest responses; and fourth quartile: 25% slowest responses). This subdivision was used in subsequent analyses of ERPs elicited by cues and targets (see below).

##### 4.5.2. ERP analysis

Artifact rejection was performed off-line by discarding epochs of the EEG that were contaminated by eye movements. Eye blinks were corrected using a time-domain linear regression method. Any remaining artifacts were discarded using an auto-adaptive averaging procedure that automatically determined the optimum signal-to-noise ratio in ERP data (Talsma, *in press*). Time-locked averages to cues and imperative stimuli were computed separately for each condition of interest.

In a first analysis, we isolated attentional orienting-related processes by comparing cue-triggered ERPs elicited by left and right attention-directing cues with cue-triggered ERPs elicited by non-informative cues. We also examined effects of cue validity on target processing. To this end, target-locked ERPs were computed for each of the 12 target conditions, which were defined based upon Cue Instruction (left, right, or non-informative), Stimulus Location (left or right), and Target Dot Location (left or right). All averages were computed using a time window of 2000 ms before to 3000 ms after stimulus onset. Relatively long epochs and baseline windows were chosen to facilitate the next step in the analysis. This step consisted of estimating and removing overlapping ERP activity from temporally adjacent cue and imperative stimuli using

the adjacent response (ADJAR) procedure (Woldorff, 1993).<sup>1</sup> After overlap correction, the resulting waveforms were referenced to the algebraic average of the two mastoid electrodes. These averages were digitally filtered with a non-causal, zero-phase shift running average filter of 9 points, which strongly reduces signal frequencies at and around 56 Hz at our sample frequency of 500 Hz, thus strongly reducing interference from power-line noise.

Next, for both cue- and target-related ERPs, the left and right hemisphere electrode positions of the ERPs elicited by right-visual field stimuli were interchanged. This was done in order to create topographical distribution maps where ipsilateral and contralateral activity was identically represented for left and right visual field stimuli (see Talsma and Kok, 2002 for a comparable approach). After this remapping, corresponding left and right visual field ERPs were collapsed into one data set. Hereafter, collapsed ipsi- and contralateral recording sites will be referred to by using to the combined international 10–10 electrode name, with a subscript of “i” referring to the ipsilateral and a subscript of “c” referring to the contralateral recording site (for instance P03/4c, refers to an ERP recorded at P03, and P04 locations, while these channels were contralateral to the stimulus locations).

To examine the relationship between cue-triggered orienting processes, attentional modulation of target processing, and response speed, in a second analysis, validly cued trials were subdivided into ‘fast’ (mean RT=363 ms), ‘somewhat fast’ (mean RT=363 ms), ‘somewhat slow’, and ‘slow’ trials based upon response times. For both valid cues and validly cued imperative stimuli, this resulted in four separate ERPs, one for each response time quartile (first quartile: 25% fastest responses; second quartile: 25% to 50% fastest responses; third quartile: 50% to 25% slowest responses; and fourth quartile: 25% slowest responses). To prevent this analysis from being affected by processes other than attentional orienting (i.e., for instance possible compatibility effects between the location of the target stimulus in the display and the position of the faint dot within the target stimulus), response time categorization was conducted separately of each trial type. The same post-processing steps (i.e., overlap estimation and correction, re-

<sup>1</sup> Adjar is an iterative technique that uses the originally recorded ERPs to estimate the overlapping components. It then subtracts the estimated overlap from the original ERPs, and uses the corrected ERPs in a subsequent iteration to provide a better estimate of the overlapping component. In subsequent iterations, the overlap estimates converge to increasingly identical solutions. In the present study, the ADJAR analysis was conducted several times, using a different number of iterations, which all converged to highly similar solutions. Successfully corrected ERPs are typically characterized by flat pre-stimulus baseline windows, which are indeed found for the target stimuli (which were overlapped by the preceding cue ERP response). The attentive reader may notice, however, that there is still some residual baseline drift present in the cue-elicited ERPs, resulting from a post-P300 return to baseline drift. The reason this drift was not corrected is that we had used a fixed time window between the onset of the target ERP and the onset of the cue ERP on the next trial. Considering that the trial sequence in the present experiment was fully randomized, this residual drift is present equally for all cue trial types, and therefore not considered problematic (see Talsma and Woldorff, 2005).

referencing, filtering, and remapping to ipsi- and contralateral locations) were performed as for the first analysis. No ERPs were computed for the invalid cues, or the invalidly cued imperative stimuli, in this analysis, due to a relatively low number of trials in these conditions.

#### 4.5.3. Statistical analyses

Amplitude effects on exogenous ERP components were determined using an interactive peak-determination procedure. First, peak latencies were computed separately for each subject/condition individually, using a subset of electrodes. The minimum and maximum latencies were individually adjusted, to ensure that each individual component's peak was enclosed in the search window (Talsma et al., 2007). Then, the local maximum or minimum peak was determined within this search window. In addition, mean amplitudes were computed using a small window surrounding each peak. Overall analyses of Cue Type and Cue Validity were based on the somewhat more conservative mean amplitude measures, since these are less sensitive to differences in noise level due to differing numbers of trials across conditions (Handy, 2005). In case of the analyses of response time effects on validly cued targets, the maximum peak amplitudes were used, since in these analyses all trials were composed of an approximately equal number of trials. Longer latency effects were analyzed by computing mean voltages of consecutive 20 ms latencies.<sup>2</sup>

In all cases, these parameters were subjected to a within-subjects (i.e., repeated measures) analysis of variance (ANOVA). Specific details concerning latencies, electrode selection, and exact design of each test are given in the Results section where appropriate. An alpha threshold of .05 was used, and degrees of freedom of tests containing more than 2 levels were adjusted using the Greenhouse and Geisser (1959) epsilon. In order to prevent type-I error, tests of consecutive time-windows were only considered significant when *p*-values were below the alpha threshold on at least two consecutive 20 ms windows.<sup>2</sup>

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<sup>2</sup> When testing multiple mean amplitude variables, the risk of type 1 error has to be dealt with. The significance criterion for one interval was set at .05. As approximately 20 intervals were tested, for each factor there is the expected outcome of  $20 \times 0.05 = 0.85$  that one of the intervals would show a type-I error. If the criterion of two consecutive intervals is used, this expected outcome is reduced to 0.05 ( $20 \times 0.05 \times 0.05$ ), a value equal to the a priori set alpha threshold (see also Talsma et al., 2001 for a similar argument).

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