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**Research Report**

# An ERP study of preparatory and inhibitory mechanisms in a cued saccade task

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**ARTICLE INFO**
**Article history:**

Accepted 22 February 2006

Available online 3 April 2006

**Keywords:**

Attention

Inhibition

Cueing

Eye movement

Event-related brain potential

**ABSTRACT**

The present study uses event-related potentials (ERPs) to investigate the neurophysiological correlates of the mechanisms involved in selection of locations for saccades. Participants performed a task in which both target and distractor locations were cued on a trial-by-trial basis. Participants were instructed to make an eye movement to the cued target location and to ignore elements at the distractor location. This experimental set-up allowed the investigation of the mechanisms involved in the top-down preparation and inhibition of locations for an eye movement. When comparing responses to leftward and rightward pointing cues, we observed an early directing attention negativity (EDAN) and an anterior directing attention negativity (ADAN) effect in the cue–target interval. These effects were similar to those observed in studies investigating attentional allocation, suggesting a close link between shifts of spatial attention and the preparation of eye movements. These components were followed by a late widespread contralateral negativity (LDAN) that was assumed to reflect both the oculomotor programming of the upcoming eye movement as well as attentional orienting. Furthermore, a new component was observed related to top-down inhibition of the distractor location. In response to the distractor cue, an early positivity above the right hemisphere (RLIP) was revealed. Finally, no modulations of early target-evoked ERP components were observed, suggesting that these components are unaffected when no further processing is required at the cued location.

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**1. Introduction**

In everyday life, we are continuously faced with complex visual scenes containing elements that might be relevant for our behavior. In order to process these elements, we can allocate our attention to relevant parts of the visual environment. When a visual target is expected to appear at a specific location, attention may be allocated to that location. This allocation can either be done with or without making an eye movement ('overt' vs. 'covert attention'). With respect to covert attention, Posner using his now classic cueing para-

digm showed that reaction times to visual targets are faster for spatial locations that were previously cued (Posner, 1980, 1978; Posner et al., 1978, 1980). In a typical cueing task, participants have to press manually a response key as soon as the target is presented. The target stimulus is preceded by a cue which provides information about the location of the upcoming target. In a cueing version typically referred to as "endogenous", a centrally displayed arrow points to the likely target location. Participants are instructed to use the arrow to focus their attention on the cued location before the appearance of the target. The target is then presented either at the location

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indicated by the cue or at a location that was not indicated by the cue. The typical finding is when the cue is valid (i.e. the target appears at the cued location), response times are fast and accuracy is high relative to the condition in which the cue is invalid (the target appears at the uncued location). The results therefore reveal a benefit for location cueing: shifting attention without making an eye movement results in advanced processing of targets presented at the attended location (for a review see [Corbetta and Shulman, 2002](#)).

There is an extensive ERP literature on the mechanisms related to the processing benefits of objects presented at locations to which covert attention was directed (e.g. [Mangun and Hillyard, 1991](#); [Hillyard and Munte, 1984](#); [Hillyard et al., 1998](#); [Michie et al., 1987](#)). Relatively early sensory components show larger amplitudes for stimuli presented at covertly attended locations than at unattended locations. The earliest modulations can be observed starting around 80 ms after stimulus onset (P1 and N1) and are assumed to be related to the current focus of spatial attention.

Besides studies on spatially selective processing of an attended location, there is a growing literature on the processes directly related to the actual shifts of attention ([Harter et al., 1989](#); [Eimer et al., 2002, 2003, 2005](#); [Hopf and Mangun, 2000](#); [Slagter et al., 2005](#); [Nobre et al., 2000](#); [Van Velzen and Eimer, 2003](#); [Green et al., 2005](#); [Talsma et al., 2005](#)). These studies investigated the preparatory shifts of attention during the interval between the cue and the target. In this interval, spatial attention is shifted to the likely location of the upcoming target on the basis of the information provided by the cue or the task instruction. [Harter et al. \(1989\)](#) provided the first evidence for ERP processes related to shifts of visuo-spatial attention during the cue–target period. They conducted a study involving children in which central arrows indicated the likely location of an upcoming target. A subtraction of ERP responses elicited by a leftward arrow cue from the responses to a rightward cue revealed two processes related to the covert attentional shifting. The earliest effect was a negative deflection over the hemisphere contralateral to the direction of the cue, called the early directing attention negativity (EDAN). The EDAN started 200 ms after cue onset and lasted until 400 ms past cue onset. It was hypothesized by [Harter et al. \(1989\)](#) that the EDAN might be related to a neural process associated with the processing of the cue and the subsequent direction of spatial attention.

In addition to the EDAN, a second effect was observed between 500 and 700 ms after cue onset. At posterior sites, the hemisphere contralateral to the arrow direction became more positive in comparison to the ipsilateral hemisphere. This effect was termed the late directing attention positivity (LDAP) and was assumed to reflect the modulation of the cortical excitability in regions involved in receiving the upcoming visual information. It must be noted that the LDAP is not always observed ([Harter and Anllo-Vento, 1991](#); [Yamaguchi et al., 1994, 1995](#)).

In later studies, an enhanced negativity at frontal electrodes contralateral to the direction of attentional shifts was also reported between 300 and 500 ms after cue onset (anterior directing attention negativity, ADAN: [Hopf and Mangun, 2000](#);

[Nobre et al., 2000](#)). This effect was hypothesized to be related to the contribution of frontal structures to the control of spatial attention shifts.

Recently, Eimer and colleagues showed that two of the mentioned components (ADAN, LDAP) are not only observed during preparation within the visual modality, but also when attention is directed to a location of a relevant auditory or tactile event ([Eimer et al., 2002, 2003](#)). This shows that the preparatory ERP components ADAN and LDAP might operate in a multimodal fashion and that the selection of a task-relevant location is controlled by supramodal control mechanisms (but see, [Green et al., 2005](#)). Note that no EDAN was observed for either the visual, tactile and auditory modality. Finally, a recent study revealed that, in addition to spatial attention shifts, the earlier mechanisms also control visual non-spatial allocations ([Slagter et al., 2005](#)). Only for the LDAP, which is present around 600 ms after the cue onset, differences between spatial and non-spatial attention were observed; the other ERP effects in the cue period were identical.

All these studies have examined responses to cues that indicated the likely location of an upcoming target. The cues are thought to elicit a process that activates neurons in a visual map that code for the cued location. This process of activation results in an improved performance for stimuli presented at that location. Even though most of the research on cueing has focused on ERP components that represent increased neural activity, in many situations, it may also be necessary to inhibit locations containing elements that need to be ignored. In various attentional capture studies, it has been shown that irrelevant salient singletons can indeed capture attention exogenously ([Theeuwes, 1991, 1992, 1994](#)). For example, in one of the studies by [Theeuwes \(1994\)](#), participants remained fixated in the center of the display and had to direct their attention to the only shape target singleton present in the display. In some conditions, an irrelevant new object with an abrupt onset was added to the display. The results showed an increase in reaction time when the irrelevant onset was presented suggesting that participants were not always able to inhibit the irrelevant distractor, causing a spatial attention shift to the location of the distractor. In a subsequent study, the same methodology was used in a task in which participants had to make an eye movement to the location of the target singleton ([Theeuwes et al., 1998](#)). In this so-called ‘oculomotor capture’ task, observers view displays containing a number of gray circles positioned on an imaginary circle around a central fixation point. After a certain period, all circles change color except one (the target circle). Upon the presentation of the target display, on some trials an additional irrelevant red circle is presented. In 30% to 40% of trials in which the additional onset circle is presented, participants do not first saccade to the target element but erroneously make an eye movement to the onset distractor location: the eyes are ‘captured’ by the onset distractor.

The advantage of using a paradigm in which participants have to make an eye movement instead of an attentional shift is that one can determine on the basis of the eye movement pattern how successful distractors were

inhibited. Indeed, in Theeuwes et al. (1998), in only 30 to 40% of the trials, the eyes went to the location of the irrelevant onset, suggesting that in 60 to 70% of the trials the distractor was successfully suppressed ('inhibited'). In addition, more recent evidence suggests that the eye movement trajectory can reveal the extent to which a distractor location is inhibited (for a review, see Van der Stigchel et al., in press). For instance, when two targets are in close proximity, a saccade to the target will deviate towards the distractor (Coren and Hoenig, 1972; Van der Stigchel and Theeuwes, 2005b). A similar effect can be observed in visual search experiments in which saccade trajectories tend to deviate towards a distractor (McPeck et al., 2000). In these situations, the distractor location is not successfully inhibited and the resulting saccade is an average vector to an intermediate location in between the target and the distractor location. When the target location is cued in advance, the opposite effect is observed: saccades deviate away from the distractor location (Van der Stigchel and Theeuwes, 2006; Doyle and Walker, 2001). Furthermore, Sheliga et al. (1994, 1995) showed that the allocation of attention influences the trajectory of the subsequent eye movement. Saccade trajectories deviated away from a location to which covert attention was previously allocated.

These deviations away from a location have been attributed to inhibitory mechanisms (Tipper et al., 1997; Sheliga et al., 1994). The vector theory states that when two possible target locations are in close proximity, the resulting vector will point to an intermediate location. When inhibition is applied to one of these two locations, the resulting vector will be pointed slightly away from the correct target location leading to a saccade that deviates away from the inhibited location.

A recent study has shown that location cueing as in the classic Posner cueing approach cannot only generate activation at particular location, but it can also generate inhibition. Van der Stigchel and Theeuwes (2006) showed that inhibition of a possible distractor location can already be present on the basis of the expected appearance of a distractor. In these experiments, participants knew both the location of an upcoming target and the location of an upcoming distractor. In other words, during the cue–target interval, participants were able to expect a target and a distractor at a particular location. In 80% of trials a distractor was indeed present, in the remaining 20% of trials it was not. The experiments showed that saccades deviated away from the distractor location when the distractor was present, but also when the distractor was expected but not present (although to a lesser degree). These results reveal that the mere expectation of a distractor at a specific location is sufficient to generate saccade deviations away from this location. Because there is no visual information at the location at which observers expected the distractor, the inhibition is applied purely on the basis of a top-down expectancy of the distractor.

In the present experiment, we investigated the inhibitory mechanisms in the cue–target period and during the target selection process. As in Van der Stigchel and Theeuwes (2006), the location of the target and the location

of the distractor were cued in advance. Participants had to make an eye movement to the target once it was presented. Target and distractor elements were presented simultaneously. The cues were equiluminantly colored arrows which were presented 1000–1400 ms before target and distractor presentation. The colors of the arrows indicated whether a target, a distractor or nothing would be presented at the location to which the arrows were pointing.

There are a number of possible effects that are of interest. With respect to the upcoming saccade target, we sought to replicate the effects related to shifting attention towards the target location, specifically the EDAN, ADAN, LDAP for the cue period and P1/N1 modulations in response to the target element. It is important to establish such a result because it would indicate that the attentional processes observed in classic paradigms in which participants respond manually to a target presented would also occur in paradigms in which participants have to make an eye movement. Note that in most previous experiments (i.e. Eimer et al., 2002, 2003, Slagter et al., 2005) participants were instructed to direct attention to a location in space while keeping the eyes in the center of the display, whereas in the current experiment, participants are not instructed to make an attentional shift: they simply had to make an eye movement to a designated location. Finding EDAN, ADAN and LDAP components in an eye movement task would be in line with evidence for a functional relationship between attention and eye shifts (Rizzolatti et al., 1987, 1994) and would converge with recent functional imaging data showing that the processes involved in covert shifts of attention and oculomotor processes share common functional areas in the human brain (Corbetta, 1998; Corbetta et al., 1998).

With respect to the distractors, the predictions are less straightforward. For the cue period, the different components related to the shift of covert attention are not likely to be present for distractor locations. So far, there is no evidence that covert attention is shifted to a location that is inhibited on the basis of the expectancy of an upcoming element. The only candidate might be an inhibition version of the EDAN related to a neural process associated with the processing of the cue. The LDAP and the ADAN are assumed to be related to covert attention shifts and are therefore not likely to be observed for distractor cues. For the responses to the distractor presentation itself, we hypothesize that P1/N1 components might be reduced compared to the target response because the distractor is presented at an inhibited location. Evidence from an Inhibition of Return (IOR) experiment has revealed that IOR was associated with a reduction of the amplitude of the visual P1 component (McDonald et al., 1999). Because IOR can be observed in situations in which a cued location is inhibited at longer stimulus-onset asynchronies (Klein, 2000), the same effect might be present in our paradigm for the inhibited distractor. To differentiate between activation and inhibition for these early responses to the imperative stimuli, we also included neutral prepare and neutral inhibit trials in which both lateralized locations were cued as the possible target or distractor locations.

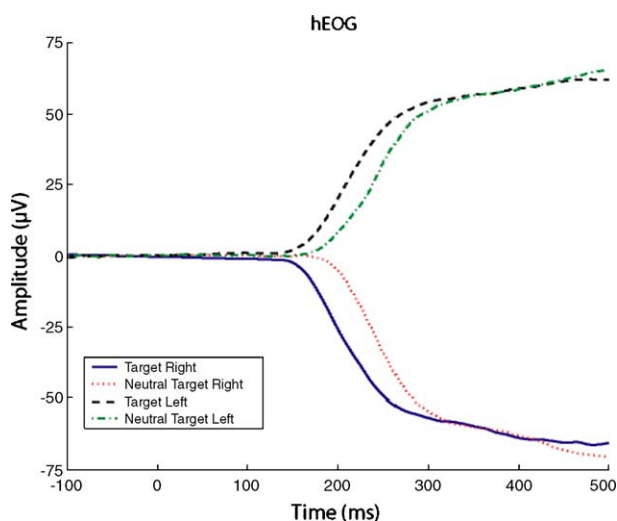
## 2. Results

### 2.1. Behavioral performance

For the cue period trials, a total of 10.2% of trials were excluded from analysis: 8.2% due to eye movements during the cue period and 2.0% due to artifacts in the EEG. For the target period trials, 9.3% of the trials were excluded: 8.5% due to eye movements around or before target onset and 0.8% due to artifacts in the EEG. With respect to the saccadic responses, Fig. 1 shows the mean horizontal EOG (hEOG) for the target conditions. Negative deflections indicate eye movements to the right. Saccade latencies in the neutral target conditions were about 50 ms longer than in the cued conditions in which there was only one possible target location.

### 2.2. ERPs in the cue period: preparation (220–330 ms)

The lower panel of Fig. 2 shows the ERPs elicited by central arrow cues requesting eye movements to the left vs. right side. They are displayed separately for the prepare left, right and both condition for posterior electrodes PO7/PO8. Starting at about 220 ms after cue onset, an enhanced negativity contralateral to the direction of the cue can be observed (EDAN). The presence of the EDAN was confirmed by a significant Cued Direction  $\times$  Hemisphere interaction ( $F(1,11) = 33.0, P < 0.001$ ) for the 220–330 ms time window. Fig. 2 also shows the mean scalp topography for the center of the tested interval (250–300 ms after cue onset) of the difference between ERPs to preparatory cues to the left and preparatory cues to the right. The EDAN to leftward pointing cues is visible as a negativity at PO8, the EDAN to rightward pointing cues is the positivity at PO7.



**Fig. 1 – Horizontal EOG for target conditions. Negative  $\mu\text{V}$  values indicate eye movements to the right and positive  $\mu\text{V}$  values represent saccades to the left. It can be seen that saccade latencies were longer in the neutrally cued conditions than in conditions in which there was only one possible target location.**

In order to determine the effect of the neutral prepare both condition, a test was conducted for each lateralized recording site to verify whether the neutral prepare ERP was different from the lateralized prepare ERPs in the EDAN latency range. At PO7, prepare both was not significantly different from prepare right ( $t(11) = 0.73, P > 0.4$ ). There was also no significant difference between prepare both and prepare left at PO8 ( $t(11) = 0.93, P > 0.3$ ).

### 2.3. ERPs in the cue period: preparation (400–500 ms)

For the period from 400 to 500 ms after cue onset, an enhanced negativity contralateral to the cued direction was observed at the frontal and central electrodes (ADAN). This ADAN was confirmed by a significant Cued Direction  $\times$  Hemisphere interaction at F3/F4 ( $F(1,11) = 17.7, P < 0.001$ ), F7/F8 ( $F(1,11) = 8.74, P < 0.02$ ) and C7/C8 ( $F(1,11) = 9.42, P < 0.02$ ). The interaction at C3/C4 was almost significant as well ( $F(1,11) = 4.57, P = 0.056$ ). The middle panel of Fig. 2 shows the mean scalp topography obtained at the center of the tested interval (425–475 ms after cue onset) of the difference between ERPs elicited by preparatory cues to the left and right hemifield. The ADAN to rightward pointing cues is the positivity peaking between F3 and C3, the ADAN to leftward pointing cues is smaller and displaced laterally.

For the neutral prepare both condition, a test was conducted at F3 and F4 in the ADAN latency range (400–500 ms) to verify whether the neutral prepare ERP was different from the lateralized prepare ERPs. At F3, prepare both was not different from prepare right ( $t(11) = 0.82, P > 0.4$ ), and there was also no significant difference between prepare both and prepare left at F4 ( $t(11) = 0.08, P > 0.9$ ).

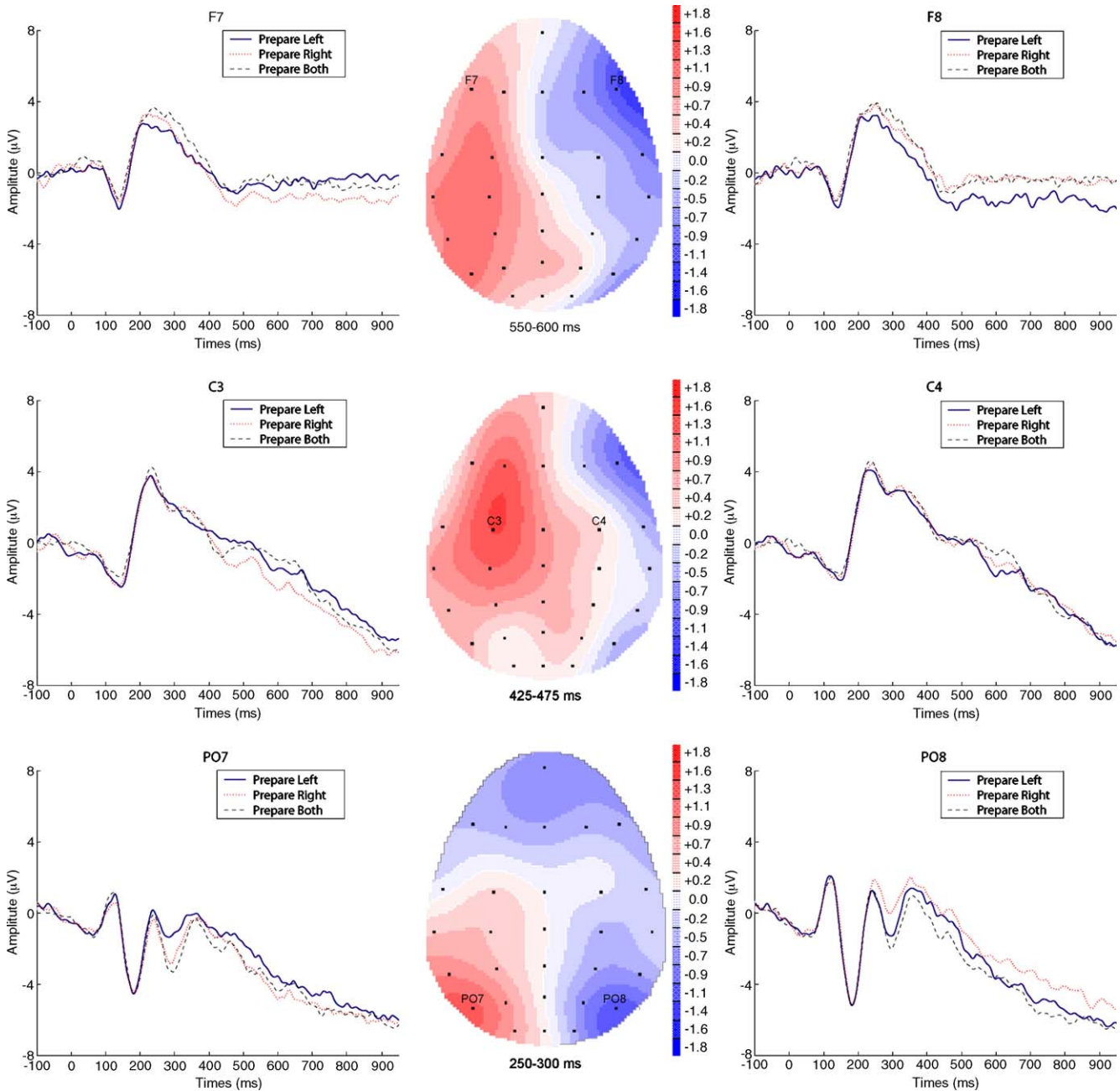
### 2.4. ERPs in the cue period: preparation (500–650 ms)

Late in the cue period, a diffuse widespread contralateral negativity was observed at lateral frontal, central and posterior sites. This was confirmed by a significant Cued Direction  $\times$  Hemisphere interaction at F7/F8 ( $F(1,11) = 14.8; P < 0.01$ ), C7/C8 ( $F(1,11) = 17.7; P < 0.01$ ) and PO7/PO8 ( $F(1,11) = 14.9; P < 0.01$ ). This effect was about equally large at all lateral sites, as there was no significant three-way interaction Electrode Site  $\times$  Cued Direction  $\times$  Hemisphere ( $F(2,22) = 0.32; P > 0.70$ ).

For the neutral prepare condition, a test was conducted for posterior lateralized recording sites to verify whether neutral prepare was different from lateralized prepare. At PO7, prepare both was not significantly different from prepare right ( $t(11) = 0.82, P > 0.4$ ). There was also no difference between prepare both and prepare left at PO8 ( $t(11) = 0.86, P > 0.4$ ).

### 2.5. ERPs in the cue period: inhibition (220–330 ms)

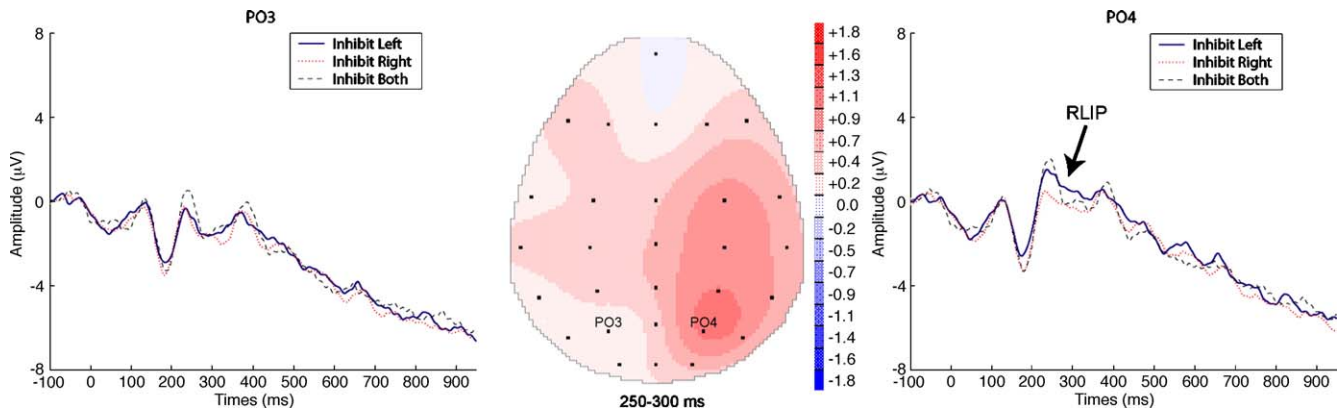
Fig. 3 shows the ERPs in response to inhibitory cues at posterior electrodes PO3/PO4. Starting about 220 ms after cue onset, an enhanced positivity contralateral to the direction of the cue can be observed at PO4. For the 220–330 ms time window, the presence of this “right-lateralized inhibition positivity” (RLIP) was confirmed by a significant main effect of Cued Direction ( $F(1,11) = 5.7, P < 0.04$ ) and a Cued Direction  $\times$  Hemisphere



**Fig. 2 – Grand-averaged ERPs elicited in the prepare conditions during the cue–target interval. These ERPs are evoked by central cues indicating the target location on the left side (solid line), on the right side (dotted line), or on both sides (dashed line). ERPs show a negativity (early directing attention negativity; EDAN; bottom row) at posterior electrodes PO7/PO8 between 220 and 330 ms contralateral to the direction of the cued hemifield. Furthermore, they show a negativity (anterior directing attention negativity; ADAN; middle row) at frontal and central electrodes between 400 and 500 ms contralateral to the direction of the cued hemifield. Finally, a late contralateral negativity (late attention directing negativity; LDAN) is present from about 500 ms onwards at all lateral electrodes. Also the mean scalp topographies for the different time intervals are shown. The negativities contralateral to the direction of the cue (EDAN, ADAN and LDAN) are reflected by negative deflections above the right hemisphere and positive deflections above the left hemisphere.**

interaction ( $F(1,11) = 11.1, P < 0.01$ ), due to the fact that it was absent at PO3. Fig. 3 also shows the mean scalp topography 250–300 ms after cue onset of the difference between ERPs elicited by inhibitory cues to the left and ERPs to inhibitory cues to the right. The RLIP is visible as the positivity at PO4; there is no accompanying negativity at PO3.

Again, for each laterized recording site, we verified whether neutral inhibition (inhibit both) was significantly different from lateralized inhibition. At PO3, inhibit both was not different from inhibit right ( $t(11) = 1.33, P > 0.20$ ), and there was also no difference between inhibit both and inhibit left at PO4 ( $t(11) = 0.31, P > 0.70$ ).



**Fig. 3** – Grand-averaged ERPs elicited in the inhibit conditions at posterior electrodes PO3/PO4 during the cue–target interval. These ERPs are evoked by central cues indicating the distractor location on the left side (solid line), on the right side (dotted line) or on both sides (dashed line). ERPs show a positivity at PO4 (right lateralized inhibition positivity; RLIP) between 220 and 330 ms contralateral to the direction of the distractor cue. Also the mean scalp topography is shown, obtained 250–300 ms after cue onset, of the difference between ERPs elicited by inhibitory cues to the left and ERPs elicited by inhibitory cues to the right. The positivity at right posterior electrodes contralateral to the direction of the cue (RLIP) is reflected by positive amplitudes above the right hemisphere. It can be seen that this effect is solely present above the right hemisphere.

## 2.6. ERPs elicited by imperative stimuli

Fig. 4 shows the mean waveforms evoked by the lateralized target and the lateralized distractor stimuli computed at the ipsi- and contralateral electrode pair P3/P4. No significant effects were observed in the P1 and N1 latency ranges ( $F < 1$ ).<sup>1</sup> For the P2 (200–230 ms), a positive enhancement ipsilateral to targets was revealed by a main effect of Condition ( $F(1,11) = 11.88$ ,  $P < 0.01$ ) and an interaction between Lateralization and Condition ( $F(1,11) = 14.10$ ;  $P < 0.01$ ). With respect to the neutral trials, no main effect of Condition ( $F < 1$ ) and no significant interaction between Lateralization and Condition were present ( $F(1,11) = 2.85$ ;  $P > 0.10$ ). In the N2 (240–280 ms) latency range, there was also a main effect of Condition ( $F(1,11) = 25.84$ ;  $P < 0.001$ ) and an interaction between Lateralization and Condition ( $F(1,11) = 11.66$ ;  $P < 0.01$ ). Similar to the P2, this effect was caused by a larger ipsilateral positivity to targets. This difference was also present for neutral trials in which a main effect of Condition was observed ( $F(1,11) = 19.52$ ;  $P < 0.01$ ) and a significant interaction ( $F(1,11) = 27.84$ ;  $P < 0.001$ ). Fig. 5 shows the scalp topography of this long-lasting ipsilateral P2/N2 difference between target and distractor stimuli obtained 250–300 ms after their onset, separately for the left and right visual field.

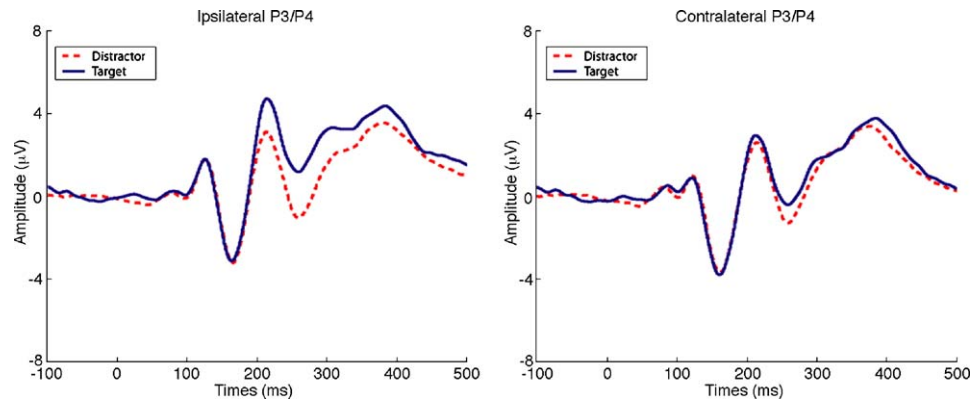
## 3. Discussion

It has been hypothesized that selection in the visual field is achieved by activating the relevant target location and de-

activating (or inhibiting) the irrelevant distractor locations (Sheliga et al., 1994; Tipper et al., 1997). The activation of a target location is mediated by a shift of spatial attention to that location. Previous experiments have investigated the electrophysiological correlates of this shift of spatial attention and have identified several distinct components related to the processing of the cue and the shift of spatial attention (Harter and Anllo-Vento, 1991; Harter et al., 1989; Eimer et al., 2002, 2005; Hopf and Mangun, 2000; Yamaguchi et al., 1994). These experiments have used cues that indicated the likely target location. However, a recent study showed that cueing a distractor location evokes the top-down inhibition of the representation of the distractor location (Van der Stigchel and Theeuwes, 2006). In the present study, we did not only want to replicate findings with respect to the electrophysiological correlates of the preparation for an upcoming target, but also wanted to explore the correlates of inhibiting the location of an upcoming distractor. Therefore, arrow cues did not only indicate the location of the upcoming target, but also of the upcoming distractor. The color of the arrows indicated the type of element that would be presented. Target and distractor were presented simultaneously at a variable time period after the cue and participants were required to saccade to the target location and to ignore the distractor. Either the target or a distractor was presented on the vertical axis or on a lateralized position, making it possible to record the lateralized brain responses to target and distractor preparation.

With respect to the preparation for a saccade target, we found an early negative deflection over posterior scalp regions contralateral to the direction of the cue, which is in line with previous findings of an EDAN (Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000). At fronto-central sites, a second negativity was observed 400 to 500 ms after cue onset, corresponding to the ADAN reported in previous studies (Hopf and Mangun, 2000; Nobre et al., 2000). This was followed by a diffuse widespread negativity at lateral frontal,

<sup>1</sup> In order to ensure that no P1/N1 effects were obtained at more lateral electrode sites, the same analysis was also performed for the ipsi- and contralateral electrode pair PO7/PO8. There was no main effect of Condition and no interaction between Lateralization and Condition ( $F < 1$ ).



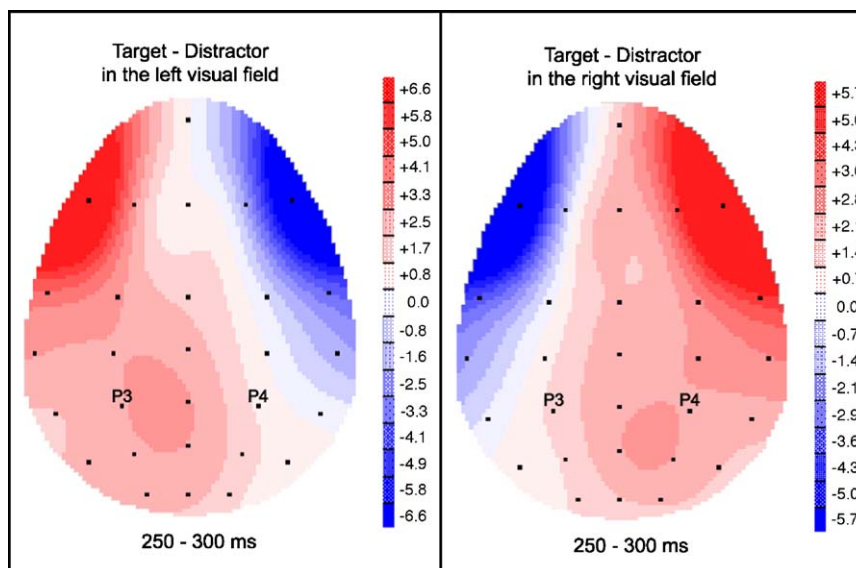
**Fig. 4 – Grand-averaged ERPs elicited by imperative stimuli at ipsi- and contralateral parietal electrodes P3/P4. These ERPs are the mean waveforms in response to cued distractors and cued targets. There are no early P1/N1 modulations, but there is an ipsilateral positive-going shift to cued targets compared to cued distractors in the P2/N2 latency range.**

central and posterior sites. Furthermore, in line with our predictions, we found a reversed effect in the EDAN latency range in response to inhibitory cues: a positive deflection in particular over right parietal regions contralateral to the direction of the cue (RLIP). These principal findings will now be discussed in turn.

The replication of ERP components related to the shifting of spatial attention towards the target location is important because in the current experiment participants were not directly instructed to make an attentional shift, but just an eye movement to the cued location. In previous studies, participants were instructed to fixate their eyes on the center of the display throughout the course of the experiment (i.e. Eimer et al., 2002, 2003; Slagter et al., 2005). The finding that similar mechanisms are observed for eye movement preparation and covert shifts of spatial attention is in line with a functional relationship between the attentional and oculomotor system (Rizzolatti et al., 1987, 1994).

### 3.1. Early-latency reflections of preparation in the cue–target interval

The earliest ERP component related to preparation was observed between 220 and 330 ms after the cue. Starting about 220 ms after cue onset, an enhanced negativity contralateral to the direction of the cue was identified at posterior electrodes. This effect is in line with previous studies that have also found an early contralateral negativity (EDAN) evoked by a cue indicating a likely target location (Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000). This EDAN was first identified by Harter et al. (1989) who hypothesized that it reflects brain activity related to the processing of the cue and the resulting allocation of covert spatial attention. The scalp distribution of this effect is in line with the involvement of parieto-occipital cortex in the control of spatial attention. There is ample evidence from single-cell recordings in monkeys (Robinson et al., 1978; Goldberg et al.,



**Fig. 5 – The mean scalp topographies of the difference between target and distractor responses obtained 250–300 ms after stimulus onset. The left panel shows responses elicited by imperative stimuli in the left visual field, the right panel shows responses to imperative stimuli in the right visual field. The ipsilateral positivity to target stimuli is largest at mid-parietal sites.**

1990; Colby et al., 1993) and cortical lesions in humans (Posner et al., 1984; Morrow and Ratcliff, 1988) for the idea that parietal cortical regions are indeed subserving spatial attention shifts. Furthermore, recent studies using fMRI have shown that the parietal cortex is involved in the top-down control of spatial attention (Corbetta and Shulman, 2002). The present results show that parieto-occipital cortex is also engaged in the control of eye movement preparation within 220 ms after the presentation of the cue.

Van Velzen and Eimer (2003) have recently hypothesized that the EDAN is not directly linked to the control of attentional shifts but instead reflects the selection of task relevant aspects of cue stimuli. According to this idea, the EDAN reflects the mere selection of relevant parts of the cue and is therefore comparable to an N2pc. This component has been interpreted as reflecting the spatial filtering of irrelevant information (Luck and Hillyard, 1994) and the selection of task-relevant stimuli (Eimer, 1996). Van Velzen and Eimer (2003) observed an EDAN regardless of the direction of the attentional shift signaled by their bilateral cues. For instance, a cue that was positioned on the left side but directing attention to the right, elicited an EDAN contralateral to the cue side (right hemisphere) and not contralateral to the side to which attention was to be shifted (left hemisphere). This contrasts with the idea that the EDAN reflects neural processes related to the shift of spatial attention. However, note that cueing experiments have indicated that the benefits of the advance knowledge about the upcoming target location does not improve much for SOAs greater than 400 ms (Remington, 1980; Remington and Pierce, 1984). This seems to suggest that shifts of attention must happen in the period before 400 ms after cue onset. Because the EDAN is the sole effect observed in this time period, it is the only candidate for the electrophysiological reflection of the shift of spatial attention (see for a similar explanation, Hopf and Mangun, 2000). Future ERP studies may help clarify this issue.

### 3.2. Intermediate-latency reflections of preparation in the cue–target interval

The second distinct ERP effect was observed starting around 400 ms after the presentation of the cue and consisted of a negativity at fronto-central sites contralateral to the direction of the cue. This component is comparable in latency and localization to the ADAN reported in earlier studies (Hopf and Mangun, 2000; Eimer et al., 2002, 2003, 2005; Slagter et al., 2005). However, the present ADAN appears asymmetric and larger over the left hemisphere. There is a focal central/frontal effect over the left hemisphere which appears smaller and displaced laterally over the right hemisphere. Still at frontal and central channels, there was a significant interaction between Hemisphere and Cued Direction without any main effect, showing that this ADAN did not differ statistically between hemispheres.

The ADAN has been interpreted as an electrophysiological correlate of processes involved in the control of allocating spatial attention in anticipation of an expected task-relevant sensory stimulus. Indeed, the frontal lobes contribute to the attentional control of voluntary focusing and the maintenance

of attention (Posner and Petersen, 1990; Pardo et al., 1991). Involvement of the frontal structures has been further revealed by studies of dorsolateral or medial frontal lobe lesions in humans (Damasio et al., 1980; De Renzi, 1982) and monkeys (Watson et al., 1973). The finding that frontal cortex structures are distinctly active also during the preparation of eye movements supports a close link between the attentional and the oculomotor system.

### 3.3. Late-latency reflections of preparation in the cue–target interval

Late in the cue–target interval (500–650 ms after cue onset), a diffuse widespread contralateral negativity was observed at lateral frontal, central and posterior sites (LDAN). It occurred as an enhanced negativity contralateral to the side of the cue. Again the effects are somewhat different over the left and right hemisphere. The left hemisphere shows a single more parietal focus, whereas the right hemisphere shows two foci of activity at lateral frontal and occipital sites. However, statistically, there was no difference between anterior and posterior sites, and no difference between hemispheres.

Some of the studies that have investigated shifts of spatial attention in anticipation of a target have found a positivity in the later parts of the cue–target interval (LDAP) (Harter et al., 1989; Nobre et al., 2000; Slagter et al., 2005). It has been generally assumed that this component reflects the modulation of excitability in cortical structures which process the upcoming visual information. Note, however, that the LDAP is not always observed (Harter and Anllo-Vento, 1991; Yamaguchi et al., 1994, 1995).

The reversal of the LDAP might be explained by the difference in response requirements between our experiment and the studies that have previously found this component. Whereas these studies have used manual or vocal responses, the current experiment is the first to have a saccade as the required response. The reversal of this component in the current set-up seems to suggest that the LDAP is specific to non-saccadic response preparation and is absent when an eye movement is required. Contrary to the LDAP, the EDAN and the ADAN components were observed and these components can therefore be regarded as a-specific to the required response type.

Because in the current experiment the upcoming event was highly predictable, it is very probable that the oculomotor response was already completely programmed during the cue–target period. This process is likely to elicit a lateralized readiness potential (LRP) (Eimer, 1995; De Jong et al., 1988) which is assumed to reflect the activation of the saccadic motor response that is about to be executed. The finding that the LDAN in the current study was widespread and not largest at central electrodes seems to contradict with the common observation that the LRP is largest at central electrodes (Gehring et al., 1992; Gratton et al., 1990). Recently, however, Talsma et al. (2005) have reported a late fronto-central negativity that was assumed to reflect processes specific to attentional orienting, such as the maintenance of attentional focus at the specified location. This fronto-central effect might also represent activity of the

Frontal Eye Fields. This brain structure plays an important role in the saccade target selection (Schall, 1991). One account of the widespread negativity in our experiment is therefore the explanation that this component consists of two distinct processes, namely a frontal and parieto-occipital component, reflecting saccadic target selection and attentional orienting, respectively.

### 3.4. Early-latency reflections of inhibition in the cue–target interval

The most important novel finding of the present study was an effect in response to the cue that indicated the location of the upcoming distractor. During a similar time period as the EDAN, a reversed effect was observed, namely a contralateral positivity starting around 220 ms after cue onset (RLIP). However, there are important differences between the EDAN and this effect with respect to their localization. The positivity evoked by the distractor cue was mainly observed at right posterior sites whereas the EDAN was observed above both hemispheres. In addition, the EDAN was maximal at PO7/PO8 sites, whereas the RLIP was maximal at PO4, indicating that these effects originate from different brain structures in parieto-occipital cortex.

The fact that the response to the distractor cue seems to be restricted to one hemisphere might be related to the hemispheric asymmetry in the control of spatial attention revealed by neuropsychological (Heilman and Van den Abell, 1980; Mesulam, 1981; Mangun et al., 1994) and imaging studies (Corbetta et al., 1993; Nobre et al., 1997; Gitelman et al., 1999). These studies indicate that the right hemisphere contributes to attentional allocations to the left and the right visual field, whereas the left posterior network contributes only to shifts to the right part of the visual field. It is possible that for inhibitory components an opposite asymmetry is responsible for the lateralization of the RLIP.

It must be noted that some studies of preparatory effects in the cue–target interval have also found components that were localized at one particular hemisphere. For instance, Nobre et al. (2000) found an ADAN-like fronto-central effect that was lateralized at the right scalp with no effect observed over left-hemisphere sites. Also the preparatory EDAN described by Hopf and Mangun (2000) and Harter and Anllo-Vento (1991) was focused at the left occipito-parietal cortex.

Which neural process this component actually reflects remains somewhat unclear. The fact that the time course of this effect resembles that of the EDAN suggests a related function as the early-latency preparatory mechanism. The reversed polarity supports the idea that the RLIP is a counterpart of the EDAN, not reflecting activation but inhibitory processes evoked by the distractor cue. The recent finding that a likely distractor location is inhibited during the cue–target interval (Van der Stigchel and Theeuwes, 2006) on the basis of a distractor cue is in line with this suggestion. Inhibition helps to successfully resolve the competition between target and distractor. The distractor cue information might trigger the mechanisms responsible for inhibiting the distractor location before the distractor presence, similar to the activation process evoked by the target cue.

### 3.5. Neutral trials in the cue–target period

We also included neutral trials in which the exact target or distractor location was uncertain. For instance in the neutral target trials, two arrows were presented that could both indicate the upcoming target location. Results show that these trials do not significantly differ from the trials in which the location of the target or the distractor was certain. For instance, preparatory responses to a target cue pointing to the right did not differ from those to a target cue pointing to both directions. The present study therefore provides further evidence for the idea that attention can be allocated to multiple locations (Van der Stigchel and Theeuwes, 2005a; Awh and Pashler, 2000; Castiello and Umiltà, 1992; Kramer and Hahn, 1995; McMains and Somers, 2004) and that saccade sequences can be programmed in parallel (Godijn and Theeuwes, 2003).

### 3.6. ERP components elicited by imperative stimuli

Contrary to earlier studies, the analysis of the ERP waveforms elicited by imperative stimuli revealed no general modulation of the P1 and N1 components to targets and distractors. This is inconsistent with the usual findings of an enhancement of the P1 and N1 to targets, which is assumed to reflect the fact that attention was shifted in response to the cue (e.g. Mangun and Hillyard, 1991; Hillyard and Munte, 1984; Hillyard et al., 1998; Michie et al., 1987). We did observe a positive shift in the P2/N2 latency range ipsilateral to the target location (200–300 ms post-target). This P2/N2 effect reflects differential processing of the target compared to the distractor and was also present for neutral trials. Scalp distribution and preliminary source localization suggest that this P2/N2 effect is generated in the medial wall of the contralateral parietal cortex and might reflect a relatively late (re)activation of target and distractor representations.

Interestingly, preparing and inhibiting an eye movement were not reflected in P1/N1 modulations of the imperative ERPs. However, the close coupling between attention and eye movements (Rizzolatti et al., 1987, 1994) and the evidence that attention precedes the eye movement towards the goal (Deubel and Schneider, 1996; Godijn and Pratt, 2002; Hoffman and Subramaniam, 1995; Irwin and Gordon, 1998; Van der Stigchel and Theeuwes, 2005a) may suggest that attention was allocated at the target location just before saccade execution. Our finding of the different cue related components also suggests that the cue was used and that spatial attention was allocated at the target location. Furthermore, saccade latencies in the lateralized target conditions were faster than in the neutral target conditions which also implies active processing of the cue resulting in a shift of spatial attention.

For these reasons, the question arises as to why a modulation of P1/N1 was absent in the current experiment. One of the things that might account for the absence of the P1/N1 modulation is the particular characteristics of the task employed. In previous studies that reported P1/N1 modulations, the target stimulus had to be actively processed in order to successfully perform the task. In the classic type of cueing ERP studies for instance, participants are cued to the left or the right visual field by means of an arrow and are required to

perform a choice reaction time about the identity of the target (i.e. whether the target stimulus was a tall or a short bar; Mangun and Hillyard, 1991). The P1/N1 modulations on valid trials compared to invalid trials are then generally explained by the facilitated sensory processing evoked by the shift of spatial attention to the cued location.

In the current experiment, the target basically did not have to be processed, because the mere detection of its presence was sufficient to correctly perform the task. The oculomotor program was programmed during the cue–target interval and the target onset just served as a go-signal for the saccade. One hypothesis is that P1/N1 modulations are only observed when the target element has to be processed up to some level. This is in line with the selection-for-action account (Posner et al., 1988; Allport, 1985; Schneider and Deubel, 2002) which assumes that selection occurs in such a way that the action can be executed optimally. In the current task, there was nothing to process at the location of the target and therefore there was no need to employ processes of early selection. Because P1/N1 modulations are assumed to reflect early attentional selection (Mangun and Hillyard, 1990, 1991), these effects may be absent in situations in which early attentional selection is not necessary for successful action performance. Note that Mangun and Hillyard (1991) conducted an experiment in which participants simply had to detect the presence of a target. Results showed only an effect on the P1 component, whereas N1 modulation was absent. This shows that the type of task indeed can result in a lack of modulation of ERPs to imperative stimuli.

#### 4. Conclusions

The present study provides some important insights in the neurophysiological correlates of preparation and inhibition of locations for eye movements. Correlates of preparation were the observed EDAN and ADAN effects which are related to shifts of spatial attention, whereas the observed late widespread negativity (LDAN) was assumed to reflect both the oculomotor programming prior to target presentation as well as attentional orienting. Because the distractor location was also cued, this spatial information could be used to inhibit the corresponding location prior to distractor presentation. A new

ERP component (RLIP) was found in response to this top-down inhibition. Future studies will have to investigate whether this effect can also be observed for other response modalities.

### 5. Experimental procedures

#### 5.1. Participants

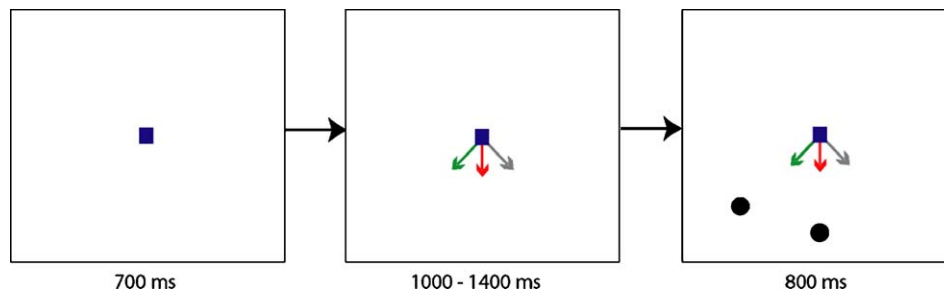
Fourteen students of the Vrije Universiteit, aged between 19 and 24 years, served as paid volunteers. Three of the participants were male. All reported normal or corrected-to-normal vision and were able to discriminate the colors used in the experiment. They were naive as to the purpose of the experiment. All participants gave their informed consent prior to their inclusion in the study. One female participant had to be excluded because of inadequate fixation in the cue–target interval (see below) and one male participant was excluded due to excessive alpha activity.

#### 5.2. Stimuli and apparatus

The stimuli were presented on a CRT monitor with a refresh rate of 100 Hz. The distance between the monitor and participant was 75 cm. Participants performed the experiment in a sound-attenuated and dimly lit room. The central fixation point was a blue box ( $0.22^\circ \times 0.22^\circ$ ). Cues were equiluminant red, green or gray arrows ( $0.69^\circ \times 0.11^\circ$ ); targets and non-targets were light gray filled circles ( $0.28^\circ$  radius). All figures were presented on a black background.

#### 5.3. Procedure and design

See Fig. 6 for an illustration of the display sequence. Each trial started with the presentation of a fixation point at the center of the screen. After 700 ms, three arrows appeared at fixation pointing straight downwards, to the lower left and to the lower right. The color of the different arrows was related to the location of the upcoming target and distractor, such that the target was presented at the location indicated by the green arrow. If the arrow had a red color, a non-target element ('distractor') was presented simultaneously with the target at the location indicated by that arrow. No object was presented



**Fig. 6** – Sequence of frames on a given trial in the present experiment. After 700 ms, the central fixation point was replaced by three equiluminant arrows pointing straight downwards, to the lower left and to the lower right. The color of the arrow cues indicated the type of the upcoming element at that location (green = target, red = distractor, gray = no element). After a variable cue period of 1000 to 1400 ms, the target and the distractor appeared and participants had to saccade to the target element.

at the location indicated by the gray arrow. The equiluminant gray arrow was included in order to avoid laterality differences between the cues, and always pointed to one side. The target and the distractor were presented after a cue period that varied randomly from 1000–1400 ms. They were presented 7° away from the central fixation point and remained on the screen for 800 ms, after which a blank screen was presented for a random period of 1300–1700 ms.

There were six conditions: prepare left, prepare right, prepare both, inhibit left, inhibit right and inhibit both. The lateralized prepare and inhibit conditions consisted of trials in which the participant knew the exact location of the upcoming target and distractor. In these trials, there was one red, one green and one gray arrow cue. Moreover, either the target or the distractor was presented at one of the lateralized locations (left or right), while the other element was presented straight downwards. For instance in the lateralized prepare condition, the target was presented on a lateralized location, while the distractor was presented on the vertical axis. In the lateralized inhibit condition, this situation was reversed; the distractor was presented on a lateralized location and the target on the vertical axis.

In the prepare both (neutral) condition, the location of the target was uncertain. A red arrow was pointing straight downwards and two green arrows were pointing to the two lateralized locations. The target was then presented at one of these two locations. In the inhibit both (neutral) condition, this situation was reversed: the location of the distractor was uncertain, but the participant knew that the target would be presented straight downwards. The sequence of trials was randomly assigned to each participant. Lateralized prepare and inhibit trials were twice as likely than neutral prepare and inhibit trials.

Participants received oral instructions before starting the experiment. They were explicitly encouraged to maintain central eye fixation and not to make an eye blink throughout the cue period. Eye movements were closely monitored during the training blocks. Whenever the EOG (see below) revealed that a participant did not maintain central eye fixation during the cue period, he or she was reminded of the necessity of continuously fixating the central fixation element. Participants were supposed to move their eyes to the target element when they detected its appearance. It was stressed that they had to make a single accurate saccade towards the target element and to keep their eyes fixated on the target element until it disappeared. The experiment consisted of a training session of 96 trials and an experimental session of 768 trials. Before the start of the experiment, participants performed a brief heterochromatic flicker fusion test (Boynton, 1979) in which they matched the luminance of the green, gray and red colors.

#### 5.4. Procedure and design

EEG was recorded from 30 sintered Ag/AgCl electrodes mounted in an elastic cap (Electro-cap International). Electrode positions were a subset of the international 10/10 system sites (FPz, F7, F3, Fz, F4, F8, C7, C3, Cz, C4, C8, CP7, CP3, CPz, CP4, CP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2, M2). All electrodes were referenced to the left mastoid (M1)

and were later digitally re-referenced to the mean between both mastoids. The vertical electro-oculogram (vEOG) was bipolarly recorded from electrodes above and below the right eye, and the horizontal electro-oculogram (hEOG) was recorded from electrodes 1 cm lateral to the external canthi of each eye. All electrode impedances were kept below 10 k $\Omega$ .

All electrophysiological signals were on-line low pass filtered (DC–70 Hz), amplified and digitized at 500 Hz. Signals were further off-line filtered (DC–40 Hz) and an automated artifact rejection procedure was applied to EOG and EEG data in order to remove trials containing saccades or EEG artifacts. Eye blinks were corrected according to the procedure by Semlitsch et al. (1986) which is the default procedure in NeuroScan's EEG analysis package. It first identifies blinks in the raw, continuous EOG data, then epochs EOG and EEG channels around each blink, and computes a "blink-locked" average for each channel. Averaging the data locked to blinks serves to reduce noise in these blink estimates, and avoids systematic contributions of stimulus or response events, as long as blinks occur sufficiently random. The blink-locked average of the vertical EOG is then correlated with the blink-locked averages of each EEG channel, in order to compute the EOG-to-EEG propagation factors. These propagation factors were plotted and inspected, and had a normal distribution over the scalp. The propagation factors were then used to subtract any blink-related activity from the EEG data. Note that this procedure was only used to correct for blinks; trials with saccades in the cue–target interval were rejected from the analysis. It was necessary to correct for blinks as they were difficult to avoid during the task given the relatively short inter-trial intervals, and rejecting the blinks would have reduced the number of remaining trials significantly.

Separate averages were computed for ERPs during the cue–target interval and for ERPs in response to subsequent imperative stimuli. For the cue period, EEG and EOG were epoched off-line into 1050 ms periods, starting 100 ms prior to cue onset and ending 950 ms after cue onset. Averages were computed relative to the 100-ms pre-cue baseline. Trials with saccades (hEOG or downward vEOG exceeding 50  $\mu$ V relative to baseline) or other artifacts (EEG exceeding  $\pm$  70  $\mu$ V at any electrode) were excluded from the analysis.

The EEG obtained in the cue–target interval was averaged separately for each condition (prepare left, prepare right, prepare both, inhibit left, inhibit right, inhibit both). Mean amplitude values were computed at posterior electrodes pairs PO7/PO8 and PO3/PO4 from 220–330, at frontal/central pairs F3/F4, F7/F8, C3/C4 and C7/C8 from 400–500 ms and at frontal/central/occipital pairs F7/F8, C7/C8 and PO7/PO8 from 500–650 ms.

The mean amplitude values were analyzed by two ANOVAs, one for preparation and one for inhibition. For both statistical tests, the factors were Hemisphere (left vs. right) and Cued Direction (left vs. right). In these analyses, the presence of lateralized preparation or inhibition effects should be reflected by Hemisphere  $\times$  Cued Direction interactions. For topographic maps, responses to cues pointing to the right were subtracted from responses to cues pointing to the left.

For the responses to the imperative stimuli, EEG and EOG were epoched off-line into 1000 ms periods, starting 500 ms prior to target onset and ending 500 ms after target onset.

Averages were computed relative to a 100-ms pre-target baseline. For the period between 500 ms before target onset and 150 ms after target onset, trials with saccades (hEOG or downward vEOG exceeding 50  $\mu\text{V}$ ) or other artifacts (EEG exceeding  $\pm 70 \mu\text{V}$  at any electrode) were excluded from analysis. After 150 ms after target onset, eye movements were supposed to be initiated and trials were only excluded if the EEG exceeded  $\pm 70 \mu\text{V}$  at any electrode location.

The EEG obtained in response to the imperative stimuli was averaged separately for each condition (target left, target right, distractor left, distractor right, neutral target left, neutral target right, neutral distractor left, neutral distractor right). Hemispheres were swapped for stimuli presented in the right visual field and electrodes were averaged, so that the right hemisphere was contralateral and the left hemisphere ipsilateral to the stimulated hemifield. Mean amplitude values were computed at electrode pairs P3/P4 and PO7/PO8 from 115–130 ms (P1), 150–180 ms (N1), 200–230 ms (P2) and 240–280 ms (N2). The mean amplitude values were analyzed by two ANOVAs, one for the lateralized prepare/inhibit trials and one for the neutral prepare/inhibit trials. For both statistical tests, the factors were Lateralization (contralateral vs. ipsilateral) and Condition (target vs. distractor). Effects of neutral trials were investigated for the time periods at which an effect of Condition was observed. We do not report trivial results due to stimulus laterality.

## Acknowledgments

We thank Niels Alting von Geusau for his technical assistance. This research was funded by a grant from NWO (Netherlands organization for Scientific Research), grant 402-01-630-PROG to Jan Theeuwes.

## REFERENCES

- Allport, A., 1985. Selection for Action: Some Behavioral and Neurophysiological Considerations of Attention and Action.
- Awh, E., Pashler, H., 2000. Evidence for split attentional foci. *J. Exp. Psychol. Hum. Percept. Perform.* 26, 834–846.
- Boynton, R.M., 1979. *Human Color Vision*. Rinehart and Winston, New York, Holt.
- Castiello, U., Umiltà, C., 1992. Splitting focal attention. *J. Exp. Psychol.* 18, 837–848.
- Colby, C.L., Duhamel, J.-R., Goldberg, M.E., 1993. The analysis of visual space by the lateral intraparietal area of the monkey: the role of extraretinal signals. In: Hicks, T.P., Molotchnikoff, S., Ono, T. (Eds.), *Progress in Brain Research*. Elsevier, Amsterdam.
- Corbetta, M., 1998. Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proc. Natl. Acad. Sci. U. S. A.* 95, 831–838.
- Corbetta, M., Shulman, G.L., 2002. Control of goal-directed and stimulus-driven attention in the brain. *Nat. Neurosci.* 3, 201–215.
- Corbetta, M., Miezin, F.M., Shulman, G.L., Petersen, S.E., 1993. A PET study of visuo-spatial attention. *J. Neurosci.* 13, 1202–1226.
- Corbetta, M., Akbudak, E., Conturo, T., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Linenweber, M.R., Peterson, S.E., Raichle, M.E., Van Essen, D.C., Shulman, G.L., 1998. A common network of functional areas for attention and eye movements. *Neuron* 21, 761–773.
- Coren, S., Hoenig, P., 1972. Effect of non-target stimuli on the length of voluntary saccades. *Percept. Mot. Skills* 34, 499–508.
- Damasio, A.R., Damasio, H., Chang, C.H., 1980. Neglect following damage to frontal lobe or basal ganglia. *Neuropsychologia* 18, 123–132.
- De Jong, R., Wierda, M., Mulder, G., Mulder, L.J.M., 1988. Use of partial information in responding. *J. Exp. Psychol. Hum. Percept. Perform.* 14, 682–692.
- De Renzi, D.E., 1982. *Disorders of Space Exploration and Cognition*. Wiley, New York.
- Deubel, H., Schneider, W.X., 1996. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vis. Res.* 36, 1827–1837.
- Doyle, M.C., Walker, R., 2001. Curved saccade trajectories: voluntary and reflexive saccades curve away from irrelevant distractors. *Exp. Brain Res.* 139, 333–344.
- Eimer, M., 1995. Stimulus-response compatibility and automatic response activation: evidence from psychophysiological studies. *J. Exp. Psychol. Hum. Percept. Perform.* 21, 837–854.
- Eimer, M., 1996. The N2pc component as an indicator of attentional selectivity. *Electroencephalogr. Clin. Neurophysiol.* 99, 225–234.
- Eimer, M., Van Velzen, J., Driver, J., 2002. Crossmodal interactions between audition, touch, and vision in endogenous spatial attention: ERP evidence on preparatory states and sensory modulations. *J. Cogn. Neurosci.* 14, 254–271.
- Eimer, M., Van Velzen, J., Forster, B., Driver, J., 2003. Shifts of attention in light and in darkness: an ERP study of supramodal attentional control and crossmodal links in spatial attention. *Cogn. Brain Res.* 15, 308–323.
- Eimer, M., Forster, B., Van Velzen, J., Prabhu, G., 2005. Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia* 43, 957–966.
- Gehring, W.J., Gratton, G., Coles, M.G.H., Donchin, E., 1992. Probability effects on stimulus evaluation and response processes. *J. Exp. Psychol. Hum. Percept. Perform.* 18, 198–216.
- Gitelman, D.R., Nobre, A.C., Parrish, T.B., Labar, K.S., Kim, Y.-H., Meyer, J.R., Mesulam, M.M., 1999. A large-scale distributed network for covert spatial attention: further anatomical delineation based on stringent behavioural and cognitive controls. *Brain* 122, 1093–1106.
- Godijn, R., Pratt, J., 2002. Endogenous saccades are preceded by shifts of visual attention: evidence from cross-saccadic priming effects. *Acta Psychol.* 110, 83–102.
- Godijn, R., Theeuwes, J., 2003. Parallel allocation of attention prior to the execution of saccade sequences. *J. Exp. Psychol. Hum. Percept. Perform.* 29, 882–896.
- Goldberg, M.E., Colby, C.L., Duhamel, J.-R., 1990. The representation of visuomotor space in the parietal lobe of the monkey. *Cold Spring Harbor Symp. Quant. Biol.* 55, 729–739.
- Gratton, G., Bosco, C.M., Kramer, A.F., Coles, M.G.H., Wickens, C.D., Donchin, E., 1990. Event-related brain potentials as indices of information extraction and response priming. *Electroencephalogr. Clin. Neurophysiol.* 75, 419–432.
- Green, J.J., Teder-Salejarvi, W.A., McDonald, J.J., 2005. Control mechanisms mediating shifts of attention in auditory and visual space: a spatio-temporal ERP analysis. *Exp. Brain Res.* 166, 358–369.
- Harter, M.R., Anllo-Vento, L., 1991. Visual-spatial attention: preparation and selection in children and adults. In: Brunia, C.H.M., Verbaten, M.N. (Eds.), *Event-Related Brain Research*. Elsevier, Amsterdam.
- Harter, M.R., Miller, S.L., Price, N.J., Lalonde, M.E., Keyes, A.L., 1989. Neural processes involved in directing attention. *J. Cogn.* 1.
- Heilman, K.M., Van den Abell, T., 1980. Right hemispheric dominance for attention: the mechanism underlying

- hemispheric asymmetries of inattention (neglect). *Neurology* 30, 327–330.
- Hillyard, S.A., Munte, T.F., 1984. Selective attention to color and location: an analysis with event-related brain potentials. *Percept. Psychophys.* 36, 185–198.
- Hillyard, S.A., Teder-Salejari, W.A., Munte, T.F., 1998. Temporal dynamics of early perceptual processing. *Curr. Opin. Neurobiol.* 8, 202–210.
- Hoffman, J.E., Subramaniam, B., 1995. Saccadic eye movements and visual selective attention. *Percept. Psychophys.* 57, 787–795.
- 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.
- Irwin, D.E., Gordon, R.D., 1998. Eye movements, attention, and transsaccadic memory. *Vis. Cogn.* 5, 127–155.
- Klein, R.M., 2000. Inhibition of return. *Trends Cogn. Sci.* 4, 138–147.
- Kramer, A.F., Hahn, S., 1995. Splitting the beam: distribution of attention over noncontiguous regions of the visual field. *Psychol. Sci.* 6, 381–386.
- Luck, S.J., Hillyard, S.A., 1994. Spatial filtering during visual search: evidence from human electrophysiology. *J. Exp. Psychol. Hum. Learn. Mem.* 20, 1000–1014.
- Mangun, G.R., Hillyard, S.A., 1990. Electrophysiological studies of visual selective attention in humans. In: Scheibel, A.B., Wechsler, A. (Eds.), *The Neurobiological Foundations of Higher Cognitive Function*. Guilford Press, New York.
- 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.
- Mangun, G.R., Hillyard, S.A., Luck, S.J., Handy, T., Plager, R., Clark, V.P., Loftus, W., Gazzaniga, M.S., 1994. Monitoring the visual world: hemispheric asymmetries and subcortical processes in attention. *J. Cogn. Neurosci.* 6, 267–275.
- McDonald, J.J., Ward, L.M., Kiehl, K.A., 1999. An event-related brain potential study of inhibition of return. *Percept. Psychophys.* 61, 1411–1423.
- McMains, S.A., Somers, D.C., 2004. Multiple spotlights of attentional selection in human visual cortex. *Neuron* 42, 677–686.
- McPeck, R.M., Skavenski, A.A., Nakayama, K., 2000. Concurrent processing of saccades in visual search. *Vis. Res.* 40, 2499–2516.
- Mesulam, M.M., 1981. A cortical network for directing attention and unilateral neglect. *Ann. Neurol.* 10, 309–325.
- Michie, P.T., Bearpark, H.M., Crawford, J.M., Glue, L.C.T., 1987. The effects of spatial selective attention on the somatosensory event-related potential. *Psychophysiology* 24, 449–463.
- Morrow, L.A., Ratcliff, G., 1988. The disengagement of covert attention and the neglect syndrome. *Psychobiology* 16, 261–269.
- Nobre, A.C., Sebestyen, G.N., Gitelman, D.R., Mesulam, M.M., Frackowiak, R.S.J., Frith, C.D., 1997. Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* 120, 515–533.
- Nobre, A.C., Sebestyen, G.N., Miniussi, C., 2000. The dynamics of shifting visuospatial attention revealed by event-related potentials. *Neuropsychologia* 38, 964–974.
- Pardo, J.V., Fox, P.T., Raichle, M.E., 1991. Localization of a human system for sustained attention by positron emission tomography. *Nature* 349, 61–64.
- Posner, M.I., 1978. *Chronometric Explorations of Mind*. Erlbaum, Hillsdale, NJ.
- Posner, M.I., 1980. Orienting of attention, the VIIth Sir Frederic Bartlett lecture. *Q. J. Exp. Psychol.* 32, 3–25.
- Posner, M.I., Petersen, S.E., 1990. The attention system of the human brain. *Annu. Rev. Neurosci.* 13, 25–42.
- Posner, M.I., Nissen, M.J., Ogden, W.C., 1978. Attended and unattended processing modes: the role of set for spatial location. In: Pick, H., Saltzman, E. (Eds.), *Modes of Perceiving and Processing Information*. Lawrence Erlbaum, Hillsdale, NJ.
- Posner, M.I., Davidson, B.J., Snyder, C.R.R., 1980. Attention and the detection of signals. *J. Exp. Psychol. Gen.* 109, 160–174.
- Posner, M.I., Walker, J.A., Friedrich, F.J., Rafal, R.D., 1984. Effects of parietal injury on covert orienting of attention. *J. Neurosci.* 4, 1863–1874.
- Posner, M.I., Petersen, S.E., Fox, P.T., Marcus, F., Raichle, M.E., 1988. Localization of cognitive operations in the human brain. *Science* 240, 1626–1631.
- Remington, R.W., 1980. Attention and saccadic eye movements. *J. Exp. Psychol. Hum. Percept. Perform.* 6, 729–744.
- Remington, R.W., Pierce, L., 1984. Moving attention: evidence for time-invariant shifts of visual selective attention. *Percept. Psychophys.* 35, 393–399.
- Rizzolatti, G., Riggio, L., Dascola, I., Umiltà, C., 1987. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25, 31–40.
- Rizzolatti, G., Riggio, L., Sheliga, B.M., 1994. Space and selective attention. In: Umiltà, C., Moscovitch, M. (Eds.), *Attention and Performance XIV*. MIT Press.
- Robinson, D.L., Goldberg, M.E., Stanton, G.B., 1978. Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J. Neurophysiol.* 41, 910–932.
- Schall, J.D., 1991. Neuronal basis of saccadic eye movements. In: Leventhal, A.G. (Ed.), *Vision and Visual Dysfunction. The Neural Basis of Visual Function*, vol. 4. Macmillan Press, London.
- Schneider, W.X., Deubel, H., 2002. Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: a review of recent findings and new evidence from stimulus-driven saccade control. In: Prinz, W., Hommel, B. (Eds.), *Attention and Performance XIX: Common Mechanisms in Perception and Action*. Oxford Univ. Press, Oxford.
- Semlitsch, H.V., Anderer, P., Schuster, P., Presslich, O., 1986. A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. *Psychophysiology* 23, 695–703.
- Sheliga, B.M., Riggio, L., Rizzolatti, G., 1994. Orienting of attention and eye movements. *Exp. Brain Res.* 98, 507–522.
- Sheliga, B.M., Riggio, L., Rizzolatti, G., 1995. Spatial attention and eye movements. *Exp. Brain Res.* 105, 261–275.
- Slagter, H.A., Kok, A., Mol, N., Kenemans, J.L., 2005. Spatio-temporal dynamics of top-down control: directing attention to location and/or color as revealed by ERPs and source modeling. *Cogn. Brain Res.* 22, 333–348.
- 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.
- Theeuwes, J., 1991. Exogenous and endogenous control of attention: the effect of visual onsets and offsets. *Percept. Psychophys.* 49, 83–90.
- Theeuwes, J., 1992. Perceptual selectivity for color and form. *Percept. Psychophys.* 51, 599–606.
- Theeuwes, J., 1994. Stimulus-driven capture and attentional set: selective search for color and visual abrupt onsets. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 799–806.
- Theeuwes, J., Kramer, A.F., Hahn, S., Irwin, D.E., 1998. Our eyes do not always go where we want them to go: capture of eyes by new objects. *Psychol. Sci.* 9, 379–385.
- Tipper, S.P., Howard, L.A., Jackson, S.R., 1997. Selective reaching to grasp: evidence for distractor interference effects. *Vis. Cogn.* 4, 1–38.
- Van der Stigchel, S., Theeuwes, J., 2005a. The influence of attending to multiple locations on eye movements. *Vis. Res.* 45, 921–927.

- Van der Stigchel, S., Theeuwes, J., 2005b. Relation between saccade trajectories and spatial distractor locations. *Cogn. Brain Res.* 25, 579–582.
- Van der Stigchel, S., Theeuwes, J., 2006. Our eyes deviate away from a location where a distractor is expected to appear. *Exp. Brain Res.* 169, 338–349.
- Van der Stigchel, S., Meeter, M. and Theeuwes, J., in press. Eye movement trajectories and what tell us. *Neurosci. Biobehav. Rev.*
- 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.
- Watson, R.T., Heilman, K.M., Cauthen, J.C., King, F.A., 1973. Neglect after cingulectomy. *Neurology* 23, 1003–1007.
- Yamaguchi, S., Tsuchiya, H., Kobayashi, S., 1994. Electroencephalographic activity associated with shifts of visuospatial attention. *Brain* 117, 553–562.
- Yamaguchi, S., Tsuchiya, H., Kobayashi, S., 1995. Electrophysiologic correlates of age effects on visuospatial attention shifts. *Cogn. Brain Res.* 3, 41–49.