Research Report

Manual response preparation and saccade programming are linked to attention shifts: ERP evidence for covert attentional orienting and spatially specific modulations of visual processing

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ABSTRACT

The premotor theory of attention claims that attentional shifts are triggered during response programming, regardless of which response modality is involved. To investigate this claim, event-related brain potentials (ERPs) were recorded while participants covertly prepared a left or right response, as indicated by a precue presented at the beginning of each trial. Cues signalled a left or right eye movement in the saccade task, and a left or right manual response in the manual task. The cued response had to be executed or withheld following the presentation of a Go/Nogo stimulus. Although there were systematic differences between ERPs triggered during covert manual and saccade preparation, lateralised ERP components sensitive to the direction of a cued response were very similar for both tasks, and also similar to the components previously found during cued shifts of endogenous spatial attention. This is consistent with the claim that the control of attention and of covert response preparation are closely linked. N1 components triggered by task-irrelevant visual probes presented during the covert response preparation interval were enhanced when these probes were presented close to cued response hand in the manual task, and at the saccade target location in the saccade task. This demonstrates that both manual and saccade preparation result in spatially specific modulations of visual processing, in line with the predictions of the premotor theory.

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1. Introduction

Cognitive control mechanisms are essential for goal-directed behaviour in a complex environment, where successful performance depends on the ability to select task-relevant sensory information, to activate and modify current task sets and goals in the light of this information, and to select and execute responses that are most appropriate in a given context. Cognitive neuroscience has begun to investigate the neural correlates of these processes and has revealed a wide network of sensory-perceptual, motor, and higher-order cognitive control mechanisms, which interact in a

complex fashion to produce flexible and adaptive goal-directed action (see Ridderinkhof et al., 2004 for a recent review).

Many cognitive control functions arise from the need for selectivity in perception and action, that is, from the requirement to select and process currently relevant sensory information (selective attention), and the requirement to select, program and activate specific responses (motor control). These two central aspects of cognitive control may not be as distinct as is often assumed. The premotor theory of attention (Rizzolatti et al., 1994) assumes that the processes involved in the control of selective spatial attention and the processes responsible for selecting specific motor responses are implemented by common neural substrates. According to this theory, goal-directed movements and shifts of spatial attention are mediated by shared control structures. Attention shifts are triggered whenever these structures are activated during response preparation. In other words, the activation of specific response programs (such as plans for a saccadic eye movement) is accompanied by covert shifts of attention, even when these response programs are later inhibited, and thus do not result in the execution of a peripheral motor response.

Empirical evidence for the hypothesis that attentional shifts towards saccade target locations are triggered during saccade preparation comes from numerous sources. Behavioural studies have demonstrated superior performance for visual events at intended saccade target locations (e.g., Deubel and Schneider, 1996; Hoffman and Subramaniam, 1995; Irwin and Gordon, 1998). There is also some initial evidence that eye movement preparation has similar spatially selective attentional effects on the processing of auditory (Rorden and Driver, 1999) and tactile stimuli (Rorden et al., 2002). Functional imaging studies have uncovered considerable overlap between frontoparietal control structures that are activated during covert shifts of visual attention and during saccade preparation (Beauchamp et al., 2001; Corbetta et al., 1998; Nobre et al., 2000a; Perry and Zeki, 2000). Patient studies have demonstrated that peripheral oculomotor deficits impair spatial attention (Craighero et al., 2001; Smith et al., 2004). Transcranial magnetic stimulation (TMS) over the frontal eye fields was found to modulate attentionally guided performance in visual search tasks (Muggleton et al., 2003), and direct electrical stimulation of this area can improve monkeys' performance in spatial attention tasks (Moore and Fallah, 2001).

In summary, there is very good evidence for the existence of close links between saccade preparation and shifts of attention. However, and importantly, the premotor theory explicitly claims that response-induced attentional shifts are by no means restricted to the oculomotor domain, but are also triggered when other types of responses, such as hand movements, are being prepared (Rizzolatti et al., 1994). In support of this claim, some studies have demonstrated superior visual discrimination performance for locations close to the target of goal-directed manual movements (Deubel et al., 1998; Schiegg et al., 2003). In general, the case for links between manual response preparation and shifts of spatial attention is however currently much less convincing than the case for links between attention and oculomotor control.

In a recent study (Eimer et al., 2005), we have used event-related brain potential (ERP) measures to obtain new evidence for the claim that shifts of attention are triggered when unimanual responses are covertly prepared. In this experiment, participants had to prepare to lift their left or the right index finger (as indicated by a visual cue that was presented at the start of each trial). The prepared response had to be executed or withheld after the presentation of a visual Go/Nogo signal. To investigate whether manual response preparation results in shifts of attention towards the effector involved in the anticipated response, irrelevant tactile probe stimuli were presented during the response preparation interval to the cued or uncued hand. Early somatosensory ERP components (P90, N140) were enhanced when probes were delivered to the cued hand, suggesting that tactile–spatial attention was directed towards the response-relevant hand.

In addition to demonstrating spatially selective effects of manual response preparation on the processing of visual probe stimuli, we also obtained more direct evidence for attention shifts induced in the course of unimanual response preparation. ERPs elicited in response to cues instructing participants to prepare a left-hand response were compared to ERPs triggered by right-hand response cues in order to isolate ERP components that are sensitive to the side of a cued manual response (see Eimer et al., 2005 for more details; see also Wauschkuhn et al., 1997; Van der Lubbe et al., 2000; Verleger et al., 2000 for a similar approach). This comparison revealed an enhanced negativity at anterior electrodes contralateral to the side of the cued response between 350 and 600 ms after cue onset, which was followed by an enhanced positivity over posterior electrodes contralateral to the cued response side. The most intriguing aspect of these lateralised ERP modulations observed during manual response preparation was that they were very similar to the modulations found in earlier experiments during explicitly cued shifts of attention. In these studies, ERPs recorded in the interval between symbolic attentional cues and the onset of a subsequent lateral imperative stimulus were compared as a function of whether the cues instructed participants to initiate a leftward or rightward attentional shift (c.f., Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000b; Yamaguchi et al., 1994). At anterior recording sites, ERPs were more negative over the hemisphere contralateral to the cued attentional shift relative to ERPs elicited ipsilaterally ('Anterior Directing Attention Negativity', ADAN). This effect started about 350 ms after cue onset, and was followed by an enhanced posterior positivity over the contralateral hemisphere ('Late Directing Attention Positivity', LDAP).[1] ADAN and LDAP are usually interpreted as reflecting successive phases in the control of spatial orienting, such as the initiation of attention shifts and the preparatory activation of sensory-specific cortical areas. The fact that these components are also present during covert unimanual

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[1] A contralateral negativity triggered at short latencies over posterior sites that was reported in several ERP studies ('early direction attention negativity', EDAN) is likely to reflect the processing of non-symmetrical (i.e., arrow) cues, and not processes directly involved in the control of anticipatory attentional shifts (see Van Velzen and Eimer, 2003 for evidence).

response preparation thus strongly suggests that attention shifts are triggered by manual response programming, even in the absence of any explicit attentional instructions.[2]

The aim of the present ERP study was to investigate the claim of the premotor theory of attention that attentional shifts are triggered during covert response preparation, regardless of the response modality involved. We directly compared ERPs triggered during the preparation of unimanual responses and during the preparation of saccadic eye movements. The general task procedure used was similar to our previous experiment (Eimer et al., 2005). Participants were instructed to prepare a response on every trial, as indicated by a visual precue, and had to execute or withhold this response following a visual Go/Nogo stimulus that was presented 1100 ms after cue onset. In the manual task, they had to prepare a left-hand or right-hand response (lifting of the index finger). In the saccade task, they had to prepare a leftward or rightward eye movement instead. In both response tasks, an irrelevant visual probe stimulus was presented during the covert response preparation interval (900 ms after cue onset) with equal probability on the cued or uncued side. During the manual task, visual probes were delivered at locations close to the left or right hand. In the saccade task, probes were presented at the saccade target locations on the left or right side.

To investigate the presence of attention shifts during manual and saccade preparation, and to study any spatially specific effects of such attention shifts on the processing of visual stimuli, separate analyses were conducted for ERPs elicited by the response cues, and for ERPs triggered by the visual probe stimuli. First, we compared ERPs following cues instructing participants to prepare a left versus right response, separately for the manual task and for the saccade task. For the manual task, we expected to confirm our previous finding (Eimer et al., 2005) that lateralised ERP components elicited during instructed shifts of spatial attention (ADAN, LDAP) are also present during unimanual response preparation, thus suggesting that attentional shifts are triggered in the course of manual response programming. The critical question was whether analogous lateralised effects would also be found when participants prepared leftward or rightward saccades. Such a result would provide further supportive evidence for the claim of the premotor theory that shifts of attention are triggered during response preparation regardless of the response modality involved.

The possibility that manual and saccade preparation may both be linked to shifts of spatial attention does of course not imply that the neural mechanisms involved in the control of hand and eye movements are otherwise identical. In fact, the premotor theory of attention explicitly acknowledges the existence of anatomical and functional dissociations between attentional-motor control mechanisms that are specialised for different types of movements, and for different parts of space (Rizzolatti et al., 1994). It is known that saccade pro-

gramming and manual response preparation are both based on complex, and distinct neural networks. Eye movement control involves structures such as the frontal eye fields, supplementary eye fields, areas 9 and 46 of the dorsolateral prefrontal cortex, cingulate cortex and lateral intraparietal areas (see Pierrot-Desseilligny et al., 2004 for a review), whereas the control of manual responses is based on parieto-frontal circuits, which include regions in prefrontal areas 4 and 6 as well as specialised posterior parietal areas (see Rizzolatti et al., 1998 for a review). Single-unit studies have revealed a functional segregation of adjacent posterior parietal areas in the monkey brain that are involved in saccade planning (area LIP) and in manual response preparation (area PRR), respectively (see Snyder et al., 2000 for a review). To explore whether ERP measures might reflect such differences in the neural substrate underlying manual and saccade preparation, we also directly compared ERPs elicited during the response preparation interval in the manual and saccade task. For this comparison, waveforms triggered by left and right response cues were collapsed, in order to identify direction-unspecific ERP differences between the two tasks.

Finally, we compared ERPs triggered by the task-irrelevant visual probes as a function of whether probes were presented adjacent to the hand involved in the anticipated response or adjacent to the opposite uncued hand (for the manual task), or at the target location of an anticipated saccade versus on the contralateral uncued side (for the saccade task). These analyses of visual probe ERPs were conducted to investigate how manual and saccade preparation affect the processing of visual stimuli. Many previous ERP studies have demonstrated that visual–spatial attention results in enhancements of early sensory-specific P1 and N1 components, and in longer-latency sustained negativities for attended relative to unattended visual stimuli (Eason, 1981; Eimer, 1994; Mangun and Hillyard, 1991). Attentional modulations of sensory-specific P1 and N1 components are usually interpreted as evidence for the sensory gating of attended locations within visual perception (Mangun, 1995), while later effects are likely to reflect the impact of spatial attention on post-perceptual processes (Mangun and Hillyard, 1991). If the preparation of unimanual responses and eye movements trigger shifts of attention, as claimed by the premotor theory, similar attentional modulations should also be observed in the present study for ERPs elicited by visual probes at cued versus uncued locations. By directly comparing such effects of response preparation on visual probe ERPs between the two response tasks, it was also possible to investigate whether manual and saccade preparation are equally effective in producing spatially specific attentional modulations of visual ERPs, or whether there are systematic differences in their impact on visual processing.

2. Results

2.1. Behavioural performance

Response latencies did not differ significantly between the saccade task (393 ms) and the manual task (386 ms). A main effect of response cueing ($F(1,15) = 15.9$; $P < 0.001$) reflected the fact that responses were faster when visual probes were

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[2] Notably, ADAN and LDAP components are not just triggered during shifts of visual attention, but also when attention is directed to the location of task-relevant auditory and tactile events, suggesting that they might reflect the activity of a modality-unspecific attentional control system (Eimer and Van Velzen, 2002; Eimer et al., 2002, 2003).

presented on the cued side than when probes were delivered on the opposite uncued side. This difference was significant for saccades (389 vs. 398 ms; t(15) = 2.7; $P < 0.02$), as well as for manual responses (381 vs. 391 ms; t(15) = 3.8; $P < 0.01$). While there was no main effect of response side, a response task × response side interaction was obtained (F(1,15) = 5.6; $P < 0.04$). Subsequent analyses revealed that right responses were faster than left responses in the manual response task (377 vs. 395 ms; t(15) = 3.4; $P < 0.01$), whereas no significant RT difference was found between left and right saccades.

False Alarms occurred on 14.4% and 18.9% of all Nogo trials in the manual task and in the saccade task, respectively. Participants failed to respond on 1.6% and 1.3% of all Go trials, for the manual task and the saccade task, respectively.

2.2. ERPs triggered during covert manual and saccade preparation: lateralised effects

ERP waveforms elicited in response to cues instructing subjects to prepare a left or right manual or saccade response are shown in Fig. 1, separately for anterior sites F7/8 and F3/4 (top panel), and for posterior sites P7/8 and OL/R (bottom panel). These waveforms show the 900 ms interval following cue onset relative to a 100 ms pre-stimulus baseline, and are collapsed across Go and Nogo trials, and across trials containing a visual probe on the left or right side. Early sensory-specific visual components (P1, N1) were triggered by the cues at posterior electrodes. More importantly, and analogous to our previous ERP study of unimanual response preparation (Eimer et al., 2005), an enhanced anterior negativity contralateral to the side of the cued response (ADAN) as well as an enhanced posterior negativity contralateral to the side of the anticipated response (LDAP) appeared to be present not only in the manual task, but in the saccade task as well.

Statistical analyses confirmed these observations. In the 350–600 ms measurement interval, a significant hemisphere × cued response interaction was present at lateral anterior electrodes, F(1,15) = 15.0; $P < 0.002$, reflecting the ADAN component (see Fig. 1, top panels). There was no significant response task × hemisphere × cued response interaction across all lateral anterior sites (F(1,15) = 2.7; $P < 0.12$), and subsequent analyses confirmed the presence of significant hemisphere × cued response interactions for the manual task (F(1,15) = 21.2; $P < 0.001$) as well as for the saccade task (F(1,15) = 4.6; $P < 0.05$).[3] No significant hemisphere × cued response interactions were observed in the 350–600 ms interval for lateral central and posterior sites.

In the subsequent measurement window (600–900 ms post-cue), a significant hemisphere × cued response interaction was triggered at lateral posterior sites (F(1,15) = 18.3; $P < 0.001$), reflecting the presence of the LDAP component (see Fig. 1, bottom panels). There was no indication of any response task × hemisphere × cued response interaction (F < 1), suggesting that this component was triggered in an analogous fashion in both response tasks. This was confirmed in subsequent analyses, which revealed significant hemisphere × cued response interactions for the manual task (F(1,15) = 14.8; $P < 0.002$) and the saccade task (F(1,15) = 11.0; $P < 0.005$). No significant hemisphere × cued response interactions were present at lateral anterior and central sites.[4]

Finally, in the 900–1200 ms interval (not shown in Fig. 1), a response task × hemisphere × cued response interaction was found only at lateral central electrode pair C3/4 (F(1,15) = 11.2; $P < 0.004$). A significant hemisphere × cued response interaction was present at C3/4 in the manual task (F(1,15) = 7.9; $P < 0.02$), reflecting the emergence of the Lateralised Readiness Potential (LRP) during the later phase of the manual response preparation interval.[5] In contrast, no such effect was present at C3/4 when subjects prepared a left or right saccade (F < 1).

2.3. ERPs triggered during covert manual and saccade preparation: non-lateralised differences

While lateralised ERP components sensitive to the direction of a cued response were very similar for the manual task and the saccade task, non-lateralised ERPs differed substantially between these two tasks. This is illustrated in Fig. 2, which shows ERPs triggered during covert response preparation in the 1200 ms interval after response cue onset for the manual task (solid lines) and the saccade task (dashed lines), with waveforms collapsed across left and right cues. Initially, ERPs elicited in the manual task were more positive than ERPs in the saccade task. This difference started at about 200 ms at anterior electrodes, was present for about 400 ms, and appeared to be absent at occipital electrodes. Around the time of Go/Nogo stimulus presentation (1100 ms after cue onset), an enhanced negativity for the manual task as compared to the saccade task emerged, which was most pronounced at posterior sites, and absent at anterior electrodes.

These observations were confirmed in analyses conducted for successive 50 ms time windows throughout the 1200 ms post-cue interval. A significant main effect of response task, reflecting the fact that ERPs were more positive for the manual

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[3] Fig. 1 suggests that the ADAN component tended to be more pronounced for the manual task relative to the saccade task. Although there was no significant response task × hemisphere × cued response interaction at anterior sites, some statistical evidence for this difference was found at electrode pair F3/4. Here, a hemisphere × cued response interaction (F(1,15) = 26.6; $P < 0.001$) was accompanied by a significant response task × hemisphere × cued response interaction (F(1,15) = 4.8; $P < 0.05$). However, follow-up analyses revealed significant hemisphere × cued response interactions for both tasks (both F(1,15) > 5.9; both $P < 0.03$), thus indicating that although attenuated relative to the manual task, the ADAN was still reliably elicited in the saccade task as well.

[4] An electrode site × hemisphere × cued response interaction was found for lateral central electrodes (F(2,30) = 11.0; $P < 0.001$; ε = 0.928). Subsequent analyses revealed that the LDAP was present at CP5/6 (hemisphere × cued response: F(1,15) = 12.0; $P < 0.003$), but not at T7/8 and C3/4.

[5] The LRP is an electrophysiological indicator of unimanual response activation (see Eimer and Coles, 2003 for more details), and its emergence during later stages of the response preparation interval in the manual task demonstrates that the cued response hand was partially activated prior to the onset of the Go/Nogo stimulus. This confirms results found in other response precueing experiments (Gehring et al., 1992; Gratton et al., 1990) where the relevant response hand was specified in advance.

task than for the saccade task, was first found at anterior electrodes between 200 and 250 ms after cue onset ($F(1,15) = 7.8$; $P < 0.02$). In the analysis intervals corresponding to the 250 to 550 ms post-cue interval, main effects of response task were consistently present at anterior, central, and midline sites (all $F(1,15) > 5.3$; all $P < 0.04$), but not at posterior electrodes.[6] No differences between the two response tasks were found between 600 and 1000 ms after cue onset. However, significant differences re-emerged in the 1050–1100 ms time window. Here, an effect of response task was present at posterior electrodes ($F(1,15) = 6.8$; $P < 0.02$) and at midline sites ($F(1,15) = 5.0$; $P < 0.05$), reflecting the fact that ERPs were now more negative for the manual as compared to the saccade task (see Fig. 2). In the 1100–1150 ms time window, this difference approached significance only at posterior electrodes ($F(1,15) = 3.8$; $P < 0.08$), but was again significant in the 1150–1200 ms measurement window at posterior and midline sites ($F(1,15) = 6.1$ and 4.6; $P < 0.03$ and 0.05, respectively). No significant effects of response task were present during these time intervals at lateral anterior and central electrodes.

2.4. ERPs elicited in response to visual probe stimuli

Figs. 3 and 4 shows visual ERPs triggered by task-irrelevant visual probe stimuli in the manual task (Fig. 3) and in the saccade task (Fig. 4) in the 400 ms after probe stimulus onset, collapsed across Go and Nogo trials. Solid lines represent ERPs in response to visual probes on the cued side (adjacent to the cued response hand for the manual task, and at the cued saccade target location for the saccade task), while dashed lines show ERPs to visual probes presented on the opposite uncued side. Probe-elicited ERPs were characterised by prominent N1, P2, and N2 components. N1 amplitudes appeared to be enhanced in both tasks when visual probes were presented on the cued side. In contrast, a subsequent enhanced negativity in the N2 time range for probes on the cued versus uncued side was present for the saccade task, but appeared to be absent in the manual task. Figs. 3 and 4 also show occipital P1 components triggered by subsequent visual Go/Nogo stimuli, which were delivered 200 ms after the probes. Analyses of probe ERPs were therefore strictly limited to the time interval prior to the emergence of early visual responses to these Go/Nogo stimuli.

Statistical analyses found no significant effects of manual or saccade response cueing on P1 amplitudes (measured between 100 and 130 ms after probe onset). In contrast, response preparation strongly affected N1 components triggered by visual probe stimuli (150–200 ms post-stimulus). Main effects of response cueing were present at lateral posterior, lateral central, and lateral anterior electrodes as well as at midline sites (all $F(1,15) > 8.2$; all $P < 0.01$). As can be seen in Figs. 3 and 4, N1 amplitudes were enhanced when visual probes were delivered on the cued side, and this was the case

both for probes presented adjacent to the cued response hand in the manual task (Fig. 3), and for probes presented at the eye movement target location in the saccade task (Fig. 4). Importantly, there was no indication of any response task × response cueing interaction at any site (all $F < 1$), demonstrating that these preparation-induced N1 modulations were triggered in an equivalent fashion in the manual task and in the saccade task.

In contrast, visual probe ERPs differed reliably between response tasks in the N2 measurement window (250–330 ms after probe onset). An enhanced negativity was elicited in the saccade task when visual probes were presented within the saccade target relative to visual probes delivered on the opposite side (Fig. 4), whereas no clear N2 modulation was present in the manual task (Fig. 3). Accordingly, a significant response task × response cueing interaction was present at midline electrodes ($F(1,15) = 9.4$; $P < 0.01$), and subsequent analyses revealed a main effect of response cueing for the saccade task ($F(1,15) = 14.2$; $P < 0.002$), but not for the manual task ($F < 1$). At lateral electrodes, electrode site × response task × response cueing interactions were present ($F(2,30) = 7.6$, 5.1, and 7.8; all $P < 0.03$; $\varepsilon = 0.827$, 0.694, and 0.672, for anterior, central, and posterior electrodes, respectively). Follow-up analyses showed that there were no effects of response cueing on N2 amplitudes in the manual response task at any recording site (all $F < 1$). In contrast, enhanced N2 amplitudes were present in the saccade task at medial electrodes F3/4, FC5/6, C3/4, CP5/6, and P3/4 (all $F(1,15) > 7.3$; all $P < 0.02$), as shown in Fig. 4. In contrast, no reliable N2 modulations were elicited in the saccade task for the more lateral electrode sites F7/8, T7/8, P7/8, and OL/R.

3. Discussion

The aim of the present ERP experiment was to investigate the claim of the premotor theory of attention that covert response preparation gives rise to attentional shifts regardless of which response modality is involved. We tested this hypothesis by directly comparing ERP indicators of attentional processing during the preparation of manual responses and of saccadic eye movements. ERPs were recorded in a manual task where participants were cued to prepare a left or right manual response, and in a saccade task where they were cued to prepare a leftward or rightward saccade, prior to the presentation of a visual Go/Nogo stimulus that instructed them to either execute or withhold the prepared response.

Lateralised ERP modulations sensitive to the direction of a cued response were very similar in both tasks. An enhanced anterior negativity at electrodes contralateral to the side of the cued response emerged between 350 and 600 ms after cue onset, and was followed by an enhanced positivity over posterior electrodes contralateral to the cued response side (see Fig. 1). These two components were very similar to the effects found in our previous ERP study of covert unimanual response preparation (Eimer et al., 2005), and, importantly, to the ADAN and LDAP components found in earlier experiments which investigated ERP correlates of instructed shifts of endogenous spatial attention (Eimer et al., 2002; Harter et al., 1989; Hopf and Mangun, 2000; Nobre et al., 2000b; Yamaguchi et al., 1994).

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[6] At lateral posterior electrodes, response task × electrode site interactions were obtained between 300 and 600 ms after cue onset, and subsequent analyses revealed main effects of response task at P3/4 throughout this interval (all $F(1,15) > 4.7$; all $P < 0.05$), reflecting the fact that ERPs elicited in the manual task were more positive than ERPs in the saccade task at this electrode pair (see Fig. 2). In contrast, no such difference was present at P7/8 and OL/R.

ANTERIOR SITES
Manual Task
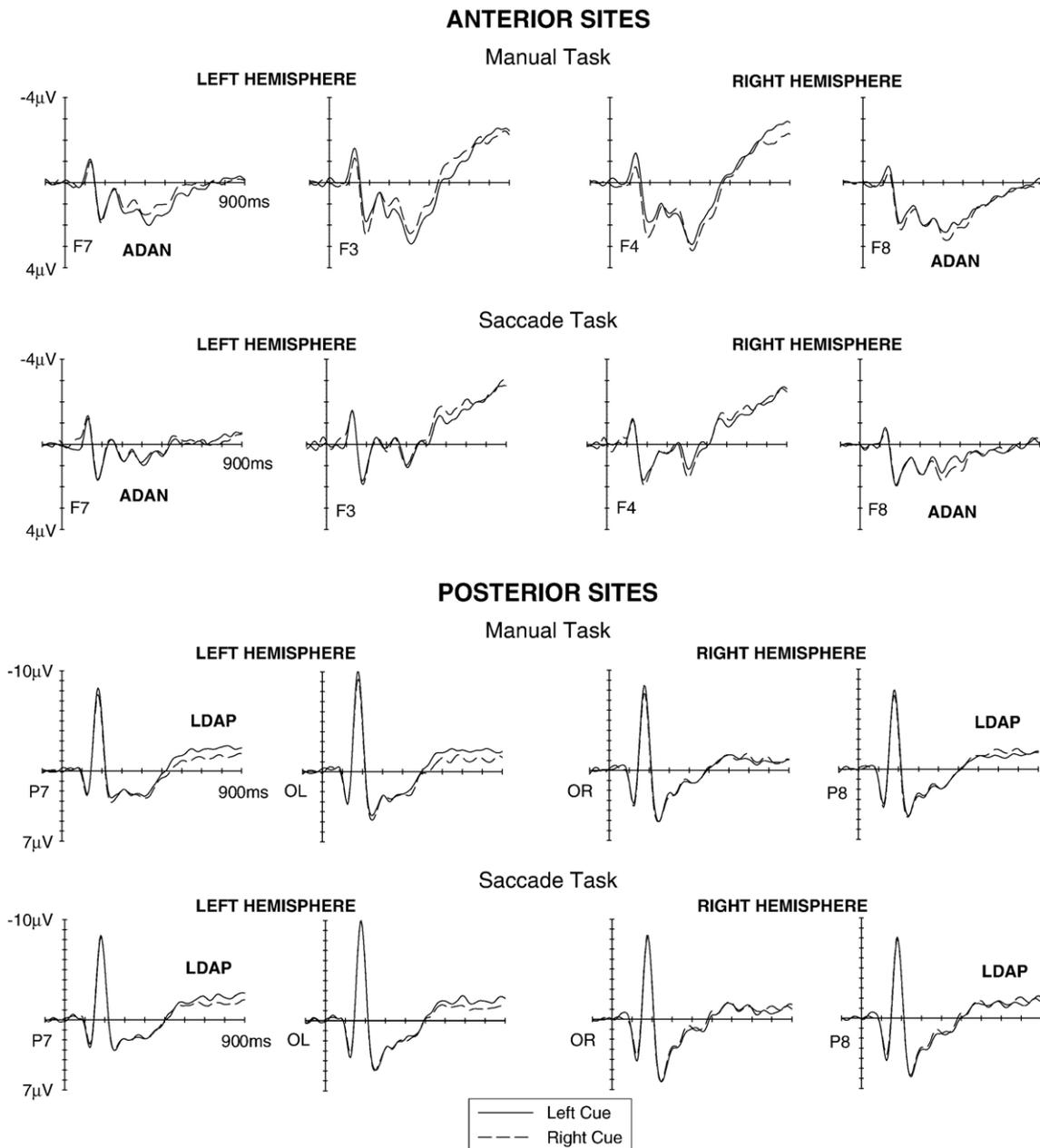
Fig. 1 – Grand-averaged ERPs elicited during covert response preparation over the left and right hemisphere at anterior electrode pairs (F7/8, F3/4, top panels) and at posterior electrode pairs (P7/8, OL/R, bottom), displayed separately for the manual task and the saccade task. Waveforms show the 900 ms interval following the onset of a visual response cue instructing participants to prepare a left response (solid lines) or right response (dashed lines), and are collapsed across trials including visual probes on the left and right side. Lateralised ERP components (ADAN: Anterior Directing Attention Negativity; LDAP: Late Directing Attention Positivity) were elicited during the covert response preparation interval.

Given that ADAN and LDAP have been interpreted as reflecting mechanisms involved in the control of attentional shifts, the finding that these components are also triggered in the course of manual and saccade preparation strongly suggests that the covert preparation of manual responses and eye movements are linked to shifts of spatial attention, as predicted by the premotor theory of attention.

It is notable that the amplitudes and latencies of the ADAN and LDAP components triggered during covert response preparation were remarkably similar for the manual and the saccade task. Although the ADAN tended to be somewhat larger in the manual task, this difference did not reach overall statistical significance. This similarity across response tasks suggests that as far as their direction-specific aspects are concerned, analogous attentional orienting processes are triggered during the preparation of manual responses and during the preparation of left and right saccades.

It is important to emphasise that although the similarity between the lateralised ERP modulations found in the present study during manual and saccade preparation and the effects

Non-lateralised ERPs elicited during covert response preparation
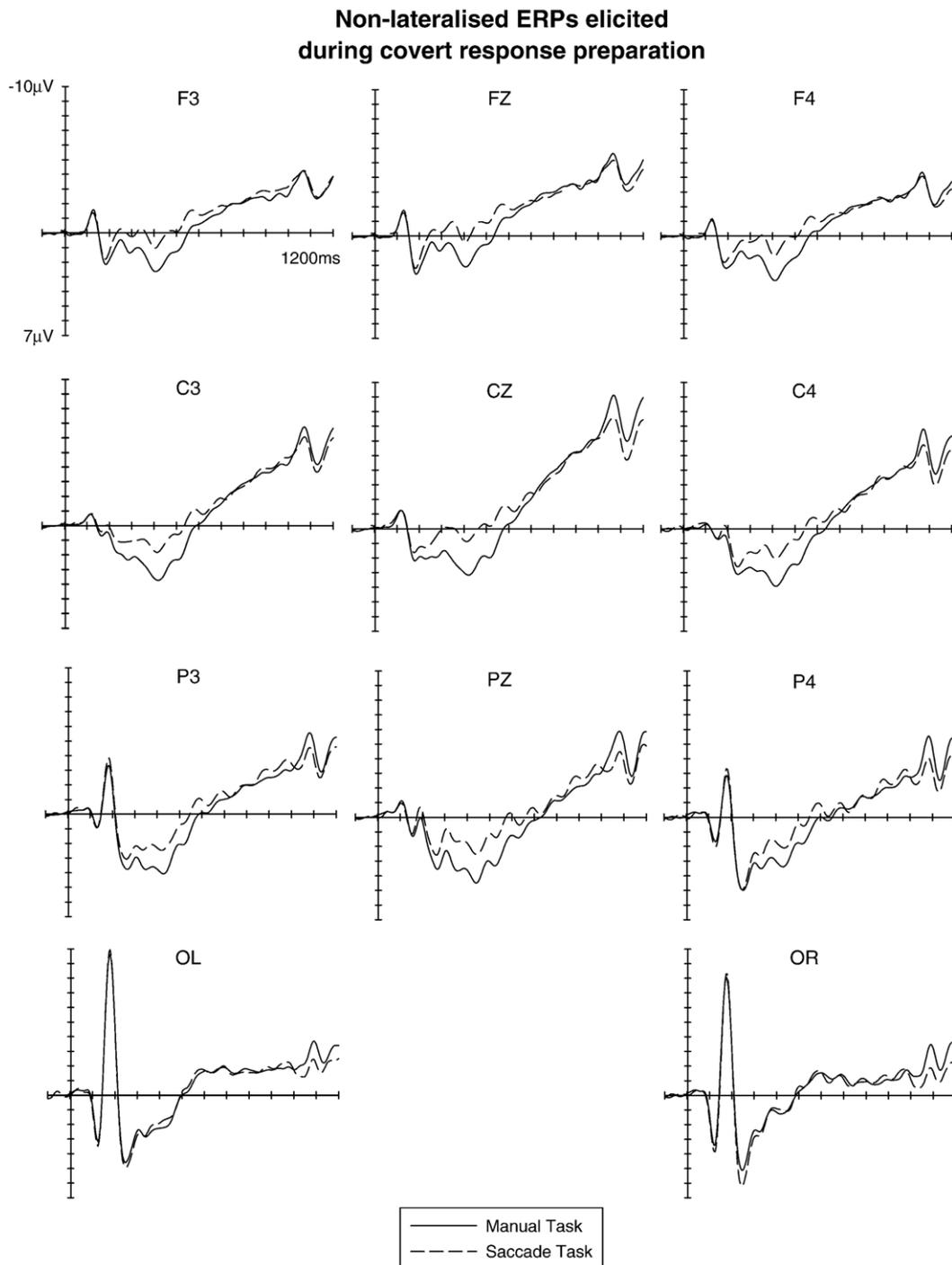
Fig. 2 – Grand-averaged ERPs elicited during covert response preparation in the manual task (solid lines) and the saccade task (dashed line), shown for the 1200 ms interval after response cue onset. Waveforms are collapsed across trials with left and right response cues.

found previously during explicitly cued shifts of spatial attention suggests close links between attention and response preparation, it does not provide direct evidence for the stronger claim of the premotor theory that these two processes are based on a common neural substrate. For example, one could argue that although attention shifts tend to be triggered during covert response preparation, the underlying mechanisms are entirely separate. In this case, the ADAN and LDAP components observed in the present study would exclusively reflect the presence of covert attentional orienting processes, which happen to be triggered during the preparation of manual responses and saccades, but not any processes involved in covert response preparation. This important issue could be further investigated in experimental studies where the direction of covert response preparation and spatial attention are manipulated independently.

ERPs to visual probes - Manual Task
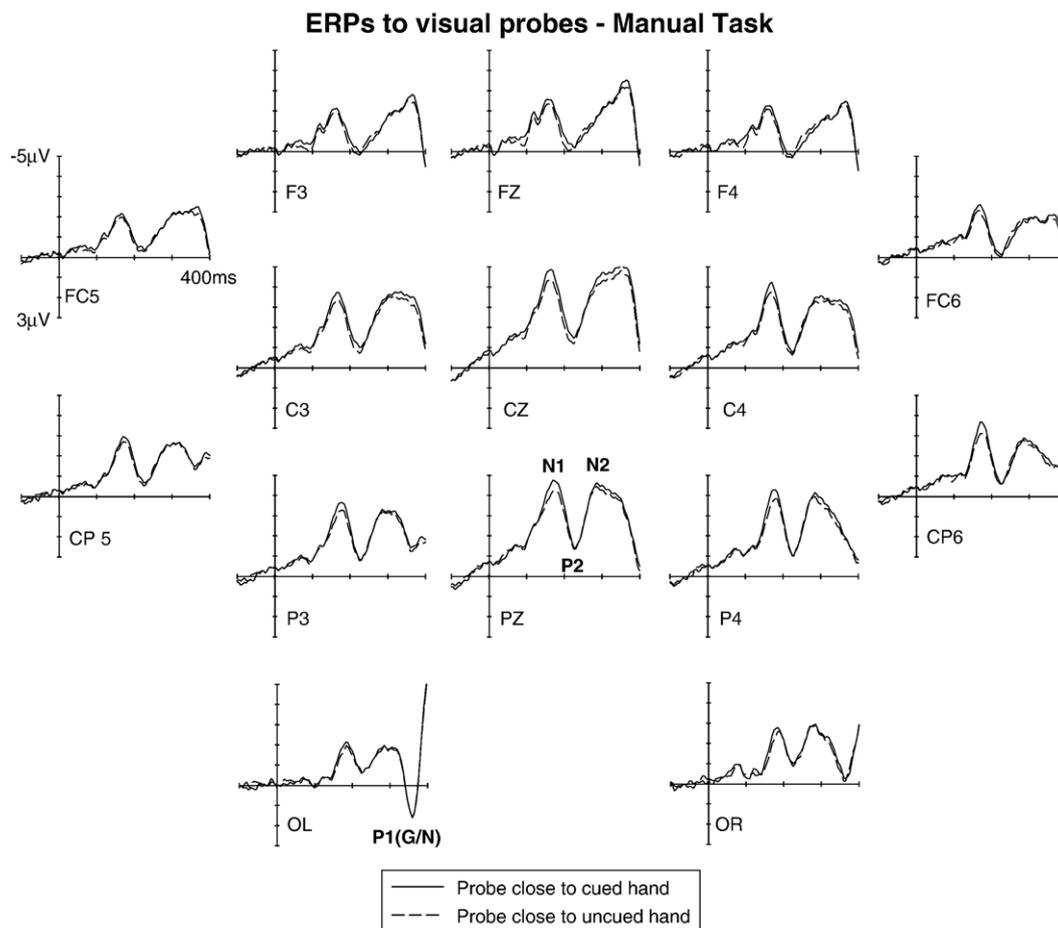
Fig. 3 – Grand-averaged visual ERPs elicited by visual probe stimuli delivered 900 ms after response cue onset in the manual task. Solid lines show ERPs triggered by visual probes presented close to the cued hand, and dashed lines show ERPs elicited by probes presented close to the uncued hand. Probe-induced components (N1, P2, N2) are followed by a P1 component at occipital electrodes, representing a visual response to the subsequently presented visual Go/Nogo stimulus (P1(G/N)).

While lateralised ERP components were very similar during manual and saccade preparation, systematic direction-unspecific differences between the two response tasks emerged in the comparison of ERP waveforms triggered during manual and saccade preparation that were averaged across trials where participants prepared a left and right response (see Fig. 2). These differences started 200 ms after cue onset at anterior electrodes, where ERPs in the manual task where more positive than ERPs in the saccade task. This differential effect then spread to lateral central sites and to midline electrodes Cz and Pz, but not to lateral occipital electrodes, and remained present until 600 ms after cue onset. A second difference of opposite polarity (more negative ERPs for the manual task relative to the saccade task) emerged 1050 ms after cue onset at posterior sites.

Any interpretation of such ERP differences between task conditions that are delivered in separate blocks has to proceed with extreme caution, as there is no neutral baseline against which they can be compared. Such differences may at least in part be due to variations of factors such as attentional load or response selection difficulty across tasks, which may result in subtle differences of generic task preparation in the cue-target interval. However, there was no evidence for any systematic

differences in the difficulty of the manual and the saccade task, as RTs did not differ between these tasks. Thus, the ERP differences observed between these two task conditions may at least in part reflect the fact that direction-unspecific aspects of saccade programming and manual response preparation are implemented by functionally and anatomically distinct brain regions. The ERP modulations observed at anterior and central sites between 200 and 600 ms after cue onset might reflect the differential recruitment of frontal brain regions specifically involved in the preparation of manual movements (such as regions of ventral premotor and primary motor cortex responsible for the control and execution of hand and finger movements) and in saccade programming (such as frontal and supplementary eye fields). The late posterior differences that emerged 1000 ms after cue onset might be linked to task-specific activations in posterior parietal cortex. Single-cell recordings (e.g., Snyder et al., 1997) have uncovered functional subdivisions between posterior parietal areas responsible for eye movement programming (area LIP) and manual response preparation (area PRR). These areas appear to be selectively activated even in the absence of advance information about response direction (Calton et al., 2002; Dickinson et al., 2003). Interestingly, Dickinson et al. (2003) found that such non-

ERPs to visual probes - Saccade Task
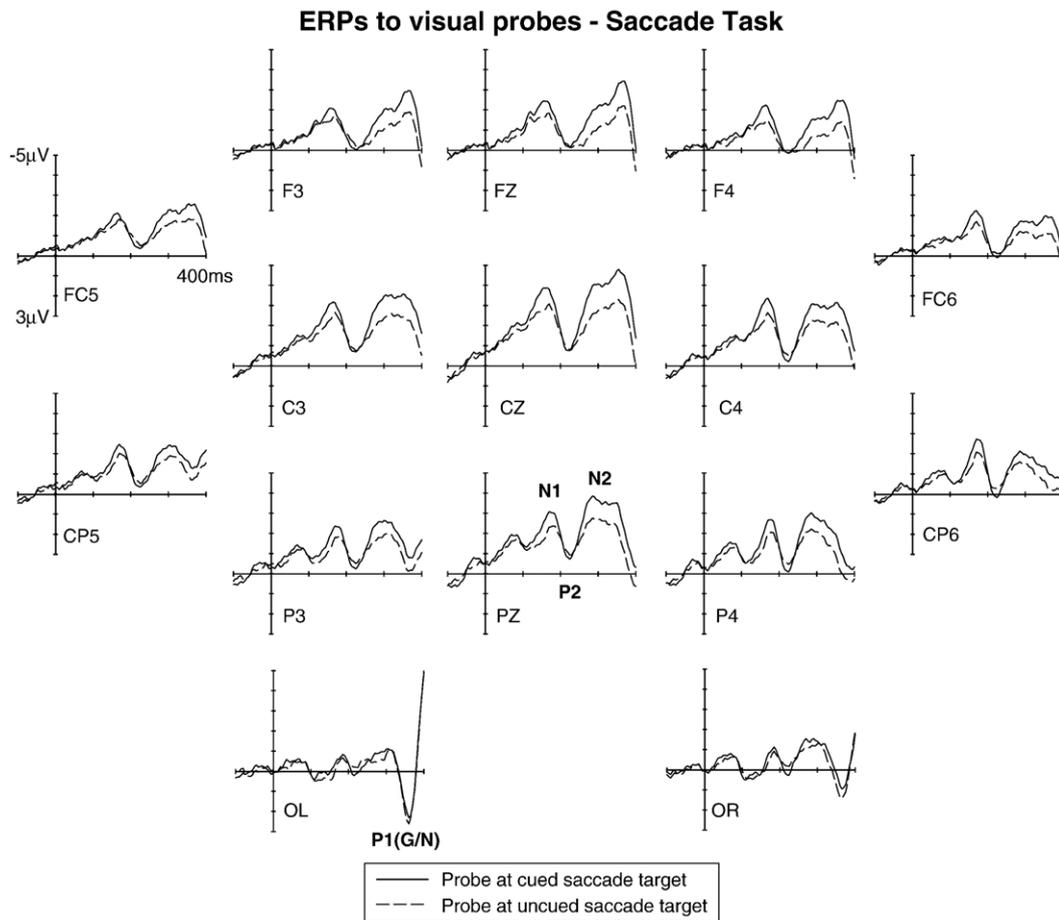
Fig. 4 – Grand-averaged visual ERPs elicited by visual probe stimuli delivered 900 ms after response cue onset in the saccade task. Solid lines show ERPs triggered by visual probes presented at the cued saccade target location, and dashed lines show ERPs elicited by probes presented at the contralateral uncued saccade target location. Probe-induced ERP components (N1, P2, N2) are followed by an occipital P1 triggered by the subsequent visual Go/Nogo stimulus (P1(G/N)).

spatial activations in effector-specific posterior parietal areas are elicited maximally during later phases of response preparation, analogous to our finding that posterior ERP differences between the manual and saccade tasks only emerged towards the end of the response preparation interval.[7]

The other aim of the present experiment was to investigate whether any shifts of attention elicited during covert manual and saccade preparation would result in systematic spatially specific modulations of visual processing. To investigate this, we recorded ERPs to task-irrelevant visual probe stimuli that were presented towards the end of the preparation interval (900 ms after cue onset). In the manual task, visual probes presented close to the cued response hand elicited enhanced N1 components when compared to probes presented adjacent

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[7] It should be noted that similar non-lateralised ERP modulations have recently been reported in other studies of attentional control (Slagter et al., 2005; Talsma et al., 2005). For example, when comparing ERPs triggered in response to spatially informative versus uninformative (neutral) cues, Talsma et al. (2005) found a broadly distributed early positivity which was followed by a central negativity. These effects were interpreted as reflecting the covert orienting and subsequent maintenance of spatial attention.

to the opposite uncued hand (see Fig. 3), thereby demonstrating that covert unimanual response preparation results in spatially specific modulations of visual processing. Very similar effects of response preparation on N1 amplitudes were also found in the saccade task. Here, visual probes presented at the cued saccade target location elicited larger N1 components relative to probes presented on the opposite uncued side (Fig. 4). There was no indication of any response task × response cueing interaction, thus indicating that these response preparation effects on visual N1 amplitudes were equivalent in size during manual and eye movement preparation.

Attentional modulations of visual N1 components have been consistently observed in ERP experiments where spatial attention was explicitly manipulated (e.g., Eason, 1981; Eimer, 1994; Mangun and Hillyard, 1991). The fact that similar modulations were also elicited in the present experiment during manual and saccade preparation thus provides additional supportive evidence for the central claim of the premotor theory of attention that the covert response preparation results in attentional shifts, irrespective of the response system involved. It should however also be noted that manual and saccade preparation had no effects on probe-induced P1 components. This result contrasts with the fact that

systematic attentional effects on P1 amplitude have been found in many previous ERP investigations of endogenous visual–spatial attention (e.g., Mangun and Hillyard, 1991). If the control of spatial attention and the processes responsible for selecting specific motor responses were based on shared neural substrates, one would expect them to have similar effects on visual processing. One possible interpretation of the absence of any P1 amplitude modulations during response preparation is that cued covert shifts of attention and of covert response preparation differ in their impact on very early extrastriate stages of visual processing. However, it should also be noted that attentional P1 modulations are strongly dependent on the demands of an attention task (e.g., Eimer, 1994). Their absence in the present study might thus primarily reflect the fact that visual probes were entirely task-irrelevant, rather than any systematic differences in the effects of cued attention and response preparation on visual processing.

While the effects of manual and saccade preparation on N1 components elicited by the visual cues were equivalent in size, a clear difference between the two response tasks was present at longer latencies. In the saccade task, probes presented at the saccade target location elicited an enhanced negativity in the N2 time range (250–330 ms after probe onset) relative to probes presented on the uncued side (Fig. 4). In contrast, no such spatially specific N2 modulation was present in the manual task. This difference, which was also reflected by response task × response cueing interaction, suggests that eye movement programming and manual response preparation differ in their impact on later stages of visual processing. While the preparation of a manual response may only have a transient impact on vision, saccade preparation appears to result in a more sustained modulation of visual processing. This difference could be related to the general fact that unlike manual response preparation, oculomotor control is itself an integral part of visual perception. It might also more specifically reflect the relative importance of visual spatial information during manual and oculomotor programming. For a simple manual task such as the finger-lifting response required in the present experiment, vision only plays a minor role for the selection of spatial response parameters, which will be largely guided by somatosensory and kinaesthetic information. In contrast, the sustained availability of visual–spatial information about saccade target locations is highly relevant during saccade programming. In other words, the differential effects of manual and saccade preparation on later stages of visual processing, as revealed by the present results, might reflect differences in the sensory-perceptual requirements between response modalities.

In summary, the present study has found new electrophysiological support for the central claim of the premotor theory of attention that covert response preparation is linked to shifts of spatial attention, irrespective of the response modality involved. We have found clear evidence for a spatially selective modulation of visual processing that is induced both during saccade preparation and during the preparation of simple unimanual responses. Furthermore, we have shown that although there are substantial direction-unspecific differences between ERPs triggered during manual and saccade preparation, ERP components sensitive to the direction of a cued

response are very similar in both tasks, and are also similar to the components previously found during cued shifts of endogenous spatial attention. Further studies are needed to find out whether shifts of attention triggered in the presence and absence of explicit response instructions are strictly analogous, or whether they differ in important aspects. As demonstrated in the present experiment, such questions can be addressed by measuring and comparing electrophysiological correlates of attentional control processes activated during response preparation and during covert attentional shifts, and by assessing their respective spatially selective effects on the processing of sensory information.

4. Experimental procedures

4.1. Subjects

Sixteen neurologically unimpaired subjects (eight females and eight males; 18–45 years old; average age: 25.8 years) participated in this study. All subjects were right-handed and had normal or corrected-to-normal vision. The experiment was performed in compliance with relevant institutional guidelines, and was approved by the Birkbeck School of Psychology ethics committee.

4.2. Stimuli, apparatus, and procedure

Subjects were seated in a dimly lit sound attenuated cabin, viewing a computer screen placed at a distance of 70 cm. All stimuli on this screen were presented in front of a black background. Hands were positioned on the left and right side, with index fingers located 25 cm to the left and right of the body midline. Each trial started with the presentation of a visual response cue at fixation (100 ms duration). In the manual task, cues indicated the hand to be used for a response to an upcoming visual Go signal. In the saccade task, cues indicated the direction of an eye movement required in response to a visual Go signal. Response cues consisted of two adjacent triangles (visual angle: 3.5° × 2.5°). One triangle was red, the other blue, and they always pointed in opposite directions ('> <' or '< >'). A central white fixation cross, located in the space between the two triangles was present throughout the experimental blocks. Response side (left or right) for each trial was signalled by the direction of one of the triangles. For half of the participants, blue triangles were relevant, and red triangles were relevant for the other half. Relevant left-pointing or right-pointing triangles were presented with equal probability to the left or right of fixation.

On each trial, a response cue was followed with a stimulus onset asynchrony (SOA) of 1100 ms by a visual Go/Nogo stimulus that was presented at fixation for 100 ms, replacing the fixation cross during this period. In 80% of all trials, a Go stimulus (the letter 'G') was presented, while in 20% of all trials, the Nogo letter 'S' (Stop) was presented instead. Both letters were presented in grey colour and subtended a visual angle of 0.8° × 0.9°. In addition, each trial also contained one task-irrelevant visual probe stimulus. Probes were presented 200 ms prior to the onset of the Go/Nogo stimulus (900 ms after

response cue onset). They consisted of a 100 ms illumination of one of two ensembles of green LEDs that were located on the left and right side. These LED ensembles consisted of six segments arranged in a circle plus one central segment. The angular size of each LED was 0.65°, the diameter of the circle was 2.4°. In the manual task, probe LEDs were positioned adjacent to each hand. In the saccade task, they were mounted to poles at an eccentricity of 39° to the left or right of fixation, at the same elevation as the central fixation cross. Participants were instructed to completely ignore these probe stimuli.

In the manual task, participants' task was to maintain central fixation, and to lift the index finger of the cued hand as fast as possible in response to the letter 'G', but to refrain from responding when the letter 'S' was presented. In the saccade task, participants were instructed to execute an eye movement to the side indicated by the cue when they detected the letter 'G', but to maintain fixation when the letter 'S' was presented instead. Saccade target locations were marked by two white rings which surrounded the left and right LED ensembles which were used to present task-irrelevant visual probes (39° eccentricity). For both tasks, the interval between the onset of a visual imperative stimulus on the preceding trial and the onset of the response cue on the subsequent trial was 2450 ms.

Twelve blocks of 80 trials each were run. The manual task and the saccade task were each delivered in six successive blocks, with task order balanced across participants. Go stimuli were presented on 64 trials per block, while Nogo stimuli were delivered on the remaining 16 trials. The irrelevant visual probe stimulus was presented with equal probability on the cued or uncued side. Thus, every block contained eight Go trials and two Nogo trials for each combination of cued response side (left vs. right) and probe stimulus location (left vs. right).

4.3. EEG recording and data analysis

EEG was recorded with Ag–AgCl electrodes and linked-earlobe reference from Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, and Oz (according to the 10–20 system), and from OL and OR (located halfway between O1 and P7, and O2 and P8, respectively). Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ, and the impedances of the earlobe reference electrodes were kept as equal as possible. Amplifier bandpass was 0.1–40 Hz, and digitisation rate was 200 Hz. Trials with eyeblinks (a voltage at Fpz exceeding ±60 μV), horizontal eye movements (a voltage at HEOG exceeding ±30 μV), or muscle artefacts (a voltage at any site exceeding ±80 μV) in the 1200 ms following response cue onset were excluded prior to data analysis. Trials with response errors (response omissions on Go trials, False Alarms on Nogo trials, response side errors, and responses executed prior to Go signal onset) were also excluded from analysis. To detect smaller systematic deviations of eye position, which would indicate residual tendencies to move the eyes towards the cued location, averaged HEOG waveforms obtained in the 1200 ms interval following cue onset in response to left versus right cues were examined separately for each participant and both response tasks. Residual HEOG deviations remained below ±3 μV for all participants and both response tasks. The absence of systematic eye movements during the response preparation interval is further illustrated in Fig. 5, which shows grand-averaged HEOG waveforms for trials with left and right cues, separately for the manual task (left) and the saccade task (right). HEOG differences in response to left versus right cues remained below 0.9 μV throughout the 1200 ms interval shown in Fig. 5.

Statistical analyses were conducted on the basis of ERP mean amplitudes obtained within predefined measurement windows during the covert response preparation interval. Separate analyses were run for ERPs elicited by response cues, and for ERPs triggered by visual probe stimuli. ERPs following response cues were averaged relative to a 100-ms baseline prior to the onset of these cues for the time interval between cue onset and 1200 ms after cue onset (100 ms after the onset of the Go/Nogo stimulus). Separate averages were computed for the manual task and the saccade task, and for trials where cues indicated an upcoming left or right response (collapsed across Go and Nogo trials, and across trials with a visual probe on the left or right side). ERP mean amplitudes
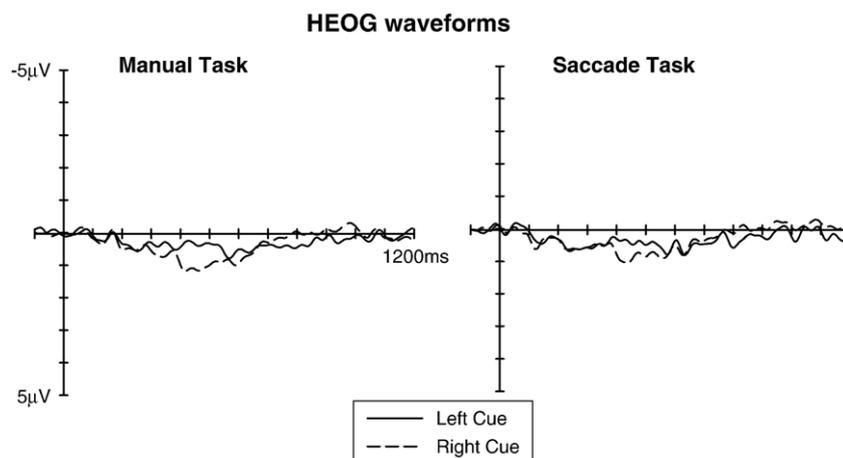
HEOG waveforms

Fig. 5 – Grand-averaged HEOG waveforms elicited in the 1200 ms interval following the onset of a visual response cue in the manual task (left) and in the saccade task (right), displayed separately for trials with left and right response cues.

were analysed with repeated measures ANOVAs, and separate analyses were conducted for lateral anterior, central, and posterior sites. Analyses investigating ERP lateralisations sensitive to the side of a cued response included the factors response task (manual vs. saccade), electrode site (F7/8 vs. F3/4 vs. FC5/6, for the anterior analysis, C3/4 vs. T7/8 vs. CP5/6, for the central analysis, and OL/R vs. P3/4 vs. P7/8, for the posterior analysis), cued response (left vs. right), and recording hemisphere (left vs. right). In these analyses, the presence of lateralised ERP components (ADAN, LDAP) is reflected by significant hemisphere × cued response interactions. As in our earlier study (Eimer et al., 2005), these analyses were based on mean amplitudes obtained within three successive post-cue latency windows between 350 and 600 ms (where the ADAN was previously observed), between 600 and 900 ms (where the LDAP component was found), and between 900 and 1200 ms.

To explore the presence of any non-lateralised ERP differences between the manual task and the saccade task, ERPs measured between cue onset and 1200 ms after cue onset were collapsed across trials with left and right cues, and were analysed within successive 50 ms measurement windows, separately for lateral anterior, lateral central, lateral posterior, and midline electrodes (Fz, Cz, Pz), for the factors response task, electrode site, and recording hemisphere (for lateral sites only).

Finally, averages were computed for ERPs triggered by visual probe stimuli. These ERPs were computed relative to a 100 ms baseline prior to probe stimulus onset for the 400 ms interval after probe onset. Separate averages were computed for all combinations of response task (manual vs. saccade), cued response (left vs. right) and probe location (left vs. right). Mean amplitudes were computed within latency windows centred on the peak amplitudes of visual P1, N1, and N2 components (P1: 100–130 ms post-stimulus; N1: 150–200 ms post-stimulus; N2: 250–330 ms post-stimulus). These mean amplitude values were analysed with repeated measures ANOVAs, separately for midline electrodes (Fz, Cz, Pz), and for lateral anterior, central, and posterior sites. Analyses included the factors response task, electrode site (defined as above), hemisphere (left vs. right, for lateral electrodes only), response cueing (probe presented on the cued vs. uncued side), and probe stimulus side (left vs. right).

Saccade reaction times (RTs) in the saccade task were measured on the basis of HEOG waveforms obtained in the 1000 ms interval following the onset of an imperative Go/Nogo stimulus. RTs were defined as the latency (in ms post-stimulus) of the first data point within this interval exceeding a threshold of ±80 μV (relative to a 100 ms baseline prior to the onset of an imperative stimulus). Saccade direction (left vs. right) was reflected by the polarity of this value. RTs in the manual task were measured via an infrared response system consisting of a transmitter and receiver LED located on either side of the middle segment of the left and right index fingers in the resting position. A response was registered when an index finger was lifted, allowing the light beam of the transmitter LED to reach the receiver LED. RTs for correct manual and saccade responses to Go stimuli were analysed in a repeated measures ANOVA for the factors response task, response side (left vs. right), and response cueing (probe presented on cued vs. uncued side). For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were applied where appropriate.

REFERENCES

Beauchamp, M.S., Petit, L., Ellmore, T.M., Ingeholm, J., Haxby, J.V., 2001. A parametric fMRI study of overt and covert shifts of visuospatial attention. NeuroImage 14, 310–321.

Calton, J.L., Dickinson, A.R., Snyder, L.H., 2002. Non-spatial, motor-specific activation in posterior parietal cortex. Nat. Neurosci. 5, 580–588.

Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., Linenweber, M.R., Petersen, 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.

Craighero, L., Carta, A., Fadiga, L., 2001. Peripheral oculomotor palsy affects orienting of visuospatial attention. NeuroReport 12, 3283–3286.

Deubel, H., Schneider, W.X., 1996. Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res. 36, 1827–1837.

Deubel, H., Schneider, W.X., Paprotta, I., 1998. Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. Visual Cogn. 5, 81–107.

Dickinson, A.R., Calton, J.L., Snyder, L.H., 2003. Nonspatial saccade-specific activation in area LIP of monkey parietal cortex. J. Neurophysiol. 90, 2460–2464.

Eason, R.G., 1981. Visual evoked potential correlates of early neural filtering during selective attention. Bull. Psychon. Soc. 18, 203–206.

Eimer, M., 1994. "Sensory gating" as a mechanism for visuospatial orienting: electrophysiological evidence from trial-by-trial cuing experiments. Percept. Psychophys. 55, 667–675.

Eimer, M., Coles, M.G.H., 2003. The lateralized readiness potential. In: Jahanshahi, M., Hallett, M. (Eds.), The Bereitschaftspotential: In Honour of Professors Deecke and Kornhuber. Kluwer Academic / Plenum, New York.

Eimer, M., Van Velzen, J., 2002. Crossmodal links in spatial attention are mediated by supramodal control processes: evidence from event-related brain potentials Psychophysiology 39, 437–449.

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.

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.

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

Hoffman, J.E., Subramaniam, B., 1995. The role of visual attention in saccadic eye movements. 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.

Mangun, G.R., 1995. Neural mechanisms of visual selective attention. Psychophysiology 32, 4–18.

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.

Moore, T., Fallah, M., 2001. Control of eye movements and spatial attention. Proc. Natl. Acad. Sci. U. S. A. 98, 1273–1276.

Muggleton, N.G., Juan, C.H., Cowey, A.Z., Walsh, V., 2003. Human frontal eye field and visual search. J. Neurophysiol. 89, 3340–3343.

Nobre, A.C., Gitelman, D.R., Dias, E.C., Mesulam, M.M., 2000a. Covert visual spatial orienting and saccades: overlapping neural systems. NeuroImage 11, 210–216.

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

Perry, R.J., Zeki, S., 2000. The neurology of saccades and covert shifts in spatial attention: an event-related fMRI study. Brain 123, 2273–2288.

Pierrot-Desseilligny, C., Milea, D., Müri, M., 2004. Eye movement control by the cerebral cortex. Curr. Opin. Neurol. 17, 17–25.

Ridderinkhof, K.R., van den Wildenberg, W.P.M., Segalowitz, S.J., Carter, C.S., 2004. Neurocognitive mechanisms of cognitive control: the role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. Brain Cogn. 56, 129–140.

Rizzolatti, G., Riggio, L., Sheliga, B., 1994. Space and selective attention. In: Umilta, C., Moscovitch, M. (Eds.), Attention and Performance XV. MIT Press, Cambridge, MA.

Rizzolatti, G., Luppino, G., Matelli, M., 1998. The organization of the cortical motor system: new concepts. Electroencephalogr. Clin. Neurophysiol. 106, 283–296.

Rorden, C., Driver, J., 1999. Does auditory attention shift in the direction of an upcoming saccade? Neuropsychologia 37, 357–377.

Rorden, C., Greene, K., Sasine, G.M., Baylis, G.M., 2002. Enhanced tactile performance at the destination of an upcoming saccade. Curr. Biol. 12, 1429–1434.

Schiegg, A., Deubel, H., Schneider, W.X., 2003. Attentional selection during preparation of prehension movements. Vis. Cogn. 10, 409–431.

Slagter, H.A., Kok, A., Mol, N., Talsma, D., Kenemans, J.L., 2005. Generating spatial and nonspatial attentional control: an ERP study. Psychophysiology 42, 428–439.

Smith, D.T., Rorden, C., Jackson, S.R., 2004. Exogenous orienting of attention depends upon the ability to execute eye movements. Curr. Biol. 14, 792–795.

Snyder, L.H., Batista, A.P., Andersen, R.A., 1997. Coding of intention in the posterior parietal cortex. Nature 386, 167–170.

Snyder, L.H., Batista, A.P., Andersen, R.A., 2000. Intention-related activity in the posterior parietal cortex: a review. Vision Res. 40, 1433–1441.

Talsma, D., Slager, 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.

Van der Lubbe, R.H.J., Wauschkuhn, B., Wascher, E., Niehoff, T., Kömpf, D., Verleger, R., 2000. Lateralized EEG components with direction information for the preparation of saccades versus finger movements. Exp. Brain Res. 132, 163–178.

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.

Verleger, R., Vollmer, C., Wauschkuhn, B., van der Lubbe, R.H.J., Wascher, E., 2000. Dimensional overlap between arrows as cueing stimuli and responses? Evidence from contra-ipsilateral differences in EEG potentials. Cogn. Brain Res. 10, 99–109.

Wauschkuhn, B., Wascher, E., Verleger, R., 1997. Lateralised cortical activity due to preparation of saccades and finger movements. Electroencephalogr. Clin. Neurophysiol. 102, 114–124.

Yamaguchi, S., Tsuchiya, H., Kobayashi, S., 1994. Electroencephalographic activity associated with shifts of visuospatial attention. Brain 11, 553–562.