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Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention

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Abstract

The premotor theory of attention claims that the preparation of goal-directed action and shifts of attention are closely linked, because they are controlled by shared sensorymotor mechanisms. Until now, support for this theory has come primarily from studies demonstrating links between saccade programming and attention shifts. The present event-related brain potential (ERP) study demonstrated that attentional orienting processes are also elicited during the covert preparation of unimanual responses. ERPs were recorded in the interval between a visual response-hand selection cue and a subsequent visual Go/Nogo signal when participants prepared to lift their left or right index finger. Lateralised ERP components elicited during response preparation were very similar to components previously observed during instructed endogenous attention shifts, indicating that analogous attentional orienting processes are activated in both cases. Somatosensory ERP components (P90, N140) were enhanced when task-irrelevant tactile probes were delivered during response preparation to the hand involved in an anticipated response, even when probes were presented well in advance of response execution. These results suggest that attentional shifts are triggered during unimanual response preparation, as predicted by the premotor theory. This link between manual response programming and attention is consistent with the hypothesis that common mechanisms are involved in the control of attention and action.

Keywords: Attention; Spatial; Response preparation; Event-related brain potentials; Somatosensory processing

1. Introduction

Theory and research in the field of selective attention has often been based on the explicit or implicit assumption that attention is a central and unitary supervisory control system, which regulates perception and action, but remains anatomically and functionally distinct from specialised peripheral mechanisms involved in sensory-perceptual and motor processing (e.g., Posner & Petersen, 1990). This traditional view has recently been challenged by investigations of dorsal frontoparietal cortical control circuits, which have revealed an extensive overlap of sensory, attentional and motor functions (cf., Andersen & Bueno, 2002; Andersen, Essick, & Siegel, 1987; Graziano, Yap, & Gross, 1994; Snyder, Batista, & Andersen, 1997). Such findings suggest that attentional control and sensorimotor processes may not be as independent as traditionally thought.

The premotor theory of attention provides an alternative to the view that attentional mechanisms are strictly separable from sensory processing and from the preparation and activation of motor responses. According to this theory, the control of goal-directed movements and the control of attention are closely linked, because they are implemented by common structures, with different control mechanisms specialised for different types of movements, and for different parts of space (Rizzolatti, Riggio, & Sheliga, 1994). At the heart of the premotor theory is the claim that shifts of attention are triggered whenever these shared control structures are activated during response preparation.

Evidence in favour of the premotor theory comes from studies demonstrating close links between the programming of saccadic eye movements and shifts of visual spatial attention. Attentional shifts towards saccade target locations

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are triggered during saccade preparation even before the eyes have begun to move (Hoffman & Subramaniam, 1995; Irwin & Gordon, 1998), resulting in superior performance to visual (Deubel & Schneider, 1996), auditory (Rorden & Driver, 1999), or tactile stimuli (Rorden, Greene, Sasine, & Baylis, 2002) at this location. Saccade trajectories are strongly affected by the current focus of visual attention (Sheliga, Riggio, & Rizzolatti, 1995), even when saccades are elicited via stimulation of the superior colliculus (Kustov & Robinson, 1996). Such findings, together with the fact that overlapping frontoparietal areas are activated during covert shifts of visual *attention* and during saccade preparation (Corbetta et al., 1998), support the premotor theory of attention, since they imply that the control of eye movements and the control of visual spatial attention are based on common mechanisms.

Unfortunately, there is as yet little evidence for similar links between shifts of attention and response preparation outside the oculomotor domain. According to the premotor theory of attention, such links are not restricted to saccade preparation, but should also be observed for other response modalities, such as during covert manual response preparation (Rizzolatti et al., 1994). Although the preparation and control of saccadic eye movements and of manual responses are likely to be mediated by separate specialised areas in posterior parietal cortex (see Andersen & Buneo, 2002, for a recent review), the premotor theory explicitly predicts both types of response programming are linked to shifts of attention. Neuropsychological evidence which implicates the manual response system in attentional processes comes from studies reporting dissociations of peripersonal (near) versus extrapersonal (far) space in neglect (cf., Berti & Frassinetti, 2000; Butler, Eskes, & Vandorpe, 2004; Halligan & Marshall, 1991; Vuilleumier, Valenza, Mayer, Reverdin, & Landis, 1998), where ‘near’ versus ‘far’ is defined with respect to the hand-reaching distance. Such dissociations have led to the suggestion that the control of spatial attention and the visual–spatial control of action in near space both involve common mechanisms in the dorsal visual stream (Goodale & Milner, 1992).

The aim of the present study was to investigate whether, analogous to attentional orienting processes induced during eye movement preparation, attention shifts are also triggered while unimanual responses are covertly prepared. Such links between manual response preparation and shifts of attention would be in line with the central claim of the premotor theory of attention that spatial orienting and response programming are mediated by common sensorymotor mechanisms, but would also be compatible with the alternative assumption that attention and response preparation are based on anatomically separate, but closely interconnected neural mechanisms. We recorded event-related brain potentials (ERPs) while participants were covertly preparing to lift their left or the right index finger, as instructed by a visual cue presented at the start of each trial. Manual responses were to be executed upon presentation of a visual Go stimulus, which appeared 1100 ms after the cue. On some trials, a Nogo stimulus was presented instead, and the cued response had to be withheld. This task required participants to continuously monitor task-relevant visual events at fixation (response cues followed by Go or Nogo stimuli), in order to ensure that the focus of visual attention would remain at fixation, and no eye movements would be triggered during the preparation interval.

ERP measures have been used in two different ways to uncover the presence of attentional orienting processes. The more common approach is to compare ERPs elicited in response to lateral sensory stimuli under conditions where these stimuli are presented at currently attended versus unattended locations. For example, when electrical or mechanical tactile stimuli are delivered to the left or right hand, and attention is focused on one designated hand, early somatosensory ERP components (N80, P100, N140) are enhanced in response to tactile stimuli presented to the currently attended hand (cf., Eimer & Driver, 2000; Eimer, Van Velzen, & Driver, 2002; Eimer, Van Velzen, Forster, & Driver, 2003; Eimer & Forster, 2003a, 2003b; García-Larrea, Lukaszewicz, & Mauguière, 1995; Hötting, Röder, & Rösler, 2003; Michie, Bearpark, Crawford, & Glue, 1987). Such findings demonstrate that directing attention to one side versus the other results in modulations of early somatosensory processing stages.

In addition to using ERP measures as indicators for the spatially selective processing of sensory stimuli at attended and unattended locations, another approach is to obtain even more direct evidence for the presence of attentional orienting processes by recording ERPs while covert shifts of spatial attention take place, that is, during the interval between cue stimuli directing attention to the left or right side and a subsequent lateral imperative stimulus (cf., Eimer et al., 2002; Eimer & Van Velzen, 2002; Eimer, Van Velzen, Forster, & Driver, 2003; Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Van Velzen, Forster, & Eimer, 2002). In these studies, ERP components sensitive to the direction of a cued attentional shift were uncovered by examining systematic differences between ERP waveforms in response to cues directing attention to the left versus right side. 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 had an onset latency of about 350 ms after cue onset, and was followed at about 500 ms post-stimulus by an enhanced posterior positivity over the contralateral hemisphere (‘late directing attention positivity’, LDAP). These lateralised components have been interpreted as reflecting successive phases in the control of spatial orienting, such as the initiation of an attention shift and the preparatory activation of sensory-specific cortical areas. Interestingly, very similar ADAN and LDAP components have recently been found during shifts of attention towards task-relevant tactile, visual, or auditory stimuli (Eimer et al., 2002), suggesting that these components may reflect the activity of a multimodal attentional control system (see Eimer

& Driver, 2001; Eimer et al., 2002 for more detailed discussion).

In the present study, both approaches were combined to uncover evidence for shifts of spatial attention elicited during covert unimanual response preparation. To uncover spatially selective modulations of sensory processing induced by the covert preparing one hand versus the other for an anticipated overt response, brief task-irrelevant tactile probe stimuli were delivered to the left or right index finger on 80% of all trials. These stimuli were delivered either 520 ms or 920 ms after cue onset (580 ms or 180 ms prior to the presentation of the imperative Go/Nogo signal), and with equal probability to the cued or uncued hand. Participants were instructed to completely ignore these stimuli. Previous studies have found that short-latency somatosensory ERP components are attenuated in response to tactile stimuli delivered to the hand involved in an action when these stimuli were delivered during (Rossini et al., 1999) or prior to (Shimazu et al., 1999; Starr & Cohen, 1985) hand movements, or even during the mental simulation of such movements (Rossini et al., 1996), suggesting that somatosensory processing is suppressed immediately before and during motor activity. Importantly, the premotor theory of attention makes exactly the opposite prediction for somatosensory ERPs elicited during covert response preparation. If shifts of attention towards the side of a task-relevant effector are elicited in the course of programming a unimanual response, ERP components in response to tactile probes delivered to the finger involved in the anticipated response should be enhanced relative to ERP components elicited by probes delivered to the opposite hand. Moreover, these modulations should be similar to the effects observed in previous studies where tactile-spatial attention was explicitly manipulated without concurrent unimanual response preparation (cf., Eimer & Forster, 2003a, 2003b; Michie et al., 1987). Tactile probes were presented either early or late during the preparation interval to investigate whether any attentional modulations might become more prominent as response preparation gradually builds up.

To obtain more direct electrophysiological evidence for the presence of any attentional shifts induced during unimanual response preparation, we also examined ERP waveforms triggered by cues which specified an upcoming left-hand versus right-hand response. In these analyses, ERPs were collapsed across trials with early and late tactile probes, and trials with probes delivered to the left and right hand. Initial evidence for lateralised ERP components sensitive to covert response preparation comes from earlier studies (Van der Lubbe et al., 2000; see also Wauschkuhn, Wascher, & Verleger, 1997) where response precues delivered full, partial, or no information about the direction (left versus right) and modality (saccade versus finger movement) of an upcoming response (see footnote 2, for further discussion). According to the premotor theory of attention, covert unimanual response activation processes not only induce shifts of spatial attention to the side relevant for an anticipated response, but these attentional shifts are equivalent to attention shifts elicited under conditions where attention is explicitly cued and thus intentionally allocated to one side versus the other. If this strong claim was correct, one would expect to find essentially the same lateralised ERP components during covert endogenous attentional orienting and during covert unimanual response preparation. Based on the findings from previous ERP studies investigating cued shifts of attention (cf., Eimer et al., 2002; Harter et al., 1989; Nobre et al., 2000), response preparation should therefore be accompanied by an enhanced frontal negativity contralateral to the side of an anticipated response (ADAN) elicited at about 350 ms after the response cue, as well as by a subsequent enhanced contralateral positivity (LDAP) at lateral posterior electrodes.

Irrespective of whether or not systematic shifts of attention (reflected by ADAN and LDAP) components are elicited during response preparation, another lateralised ERP effect should definitely be present. The response precueing procedure employed here allowed participants to partially prepare left-hand or right-hand responses prior to the onset of the imperative stimulus, and this should give rise to a lateralised readiness potential (LRP). The LRP is an electrophysiological indicator of unimanual response activation in primary motor cortex, reflected by an enhanced negativity over the motor cortex contralateral to the side of the activated response (see Eimer & Coles, 2003; Eimer, 1998, for more details). In previous response cueing experiments which employed cue-target intervals similar to the interval used in the present study, the LRP started approximately 400 ms prior to target onset (Gehring, Gratton, Coles, & Donchin, 1992; Gratton et al., 1990). Thus, we expected this component to emerge only towards the end of the response preparation interval.

2. Methods

2.1. Participants

Twelve normal subjects (five females and seven males; 22–34 years old; average age: 28.1 years) participated in this study. The experiment was performed in compliance with relevant institutional guidelines, and was approved by the School of Psychology ethics committee.

2.2. 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. Index fingers were positioned 25 cm to the left and right of the body midline. Two solenoids, which drove a metal rod with a blunt conical tip, were attached with medical tape on top of the middle segment of the index fingers. The rods made contact with the fingers whenever a current was passed through the solenoid. Tactile probe stimuli consisted of one rod contacting a finger for 6 ms. White noise (62 dB SPL) was continuously present to mask any sounds made by the tactile stimulators.

Visual response cues consisted of two adjacent triangles, presented centrally on a computer screen at a viewing distance of 55 cm (visual angle: 3.5° × 2.5°). One triangle was red, the other blue, and they always pointed in opposite directions (‘> <’ or ‘< >’). A central fixation cross, located between both triangles, was continuously present throughout the experimental blocks. Response side 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. Uppercase letters ‘G’ (Go) and ‘S’ (Stop), presented at fixation (visual angle 0.8° × 0.9°), served as Go and Nogo stimuli, respectively.

Twelve blocks of 100 trials each were run. Each trial started with a 100 ms presentation of the cue, which was followed after an interval of 1000 ms by the imperative stimulus (Go or Nogo). On 80 trials, a tactile probe stimulus was presented with equal probability to the cued or uncued hand, either early (520 ms after cue onset) or late (920 ms after cue onset) during the response preparation interval. On the remaining 20 trials, no tactile probe was presented. Participants were instructed to maintain central fixation, to entirely ignore all tactile events, and to lift the index finger of the cued hand as fast as possible in response to the letter ‘G’ (which was presented on 80 trials), but to refrain from responding when the letter ‘S’ was presented (on 20 trials per block). Manual response times were measured via an infrared response system consisting of a transmitter and receiver LED located on either side of the middle segment of each index finger in the resting position. A response was registered when the index finger was lifted, allowing the light beam of the transmitter LED to reach the receiver LED. On trials with premature responses (finger movements prior to the onset of the Go/Nogo stimulus), responses with the uncued finger, or without any response within 850 ms after a Go stimulus, an error feedback tone (1175 Hz, 50 ms duration) was presented, and these trials were excluded from analysis. The interval between a visual Go/Nogo stimulus and the onset of the response cue on the subsequent trial was 2450 ms.

2.3. *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 electrodes were kept as equal as possible. Amplifier bandpass was 0.1–40 Hz, and digitisation rate was 200 Hz. Trials with eyeblinks, horizontal eye movements, or muscle artefacts were excluded prior to data analysis.

All statistical analyses were conducted on the basis of ERP mean amplitudes obtained within specific measurement windows during the covert response preparation interval. Separate analyses were run for ERPs in response to left and right response-hand selection cues, and for ERPs elicited by tactile probe stimuli. For both sets of analyses, only trials where tactile probe stimuli were present were included. ERPs triggered by the 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 subsequently presented imperative visual stimulus). Separate averages were computed for all combinations of cued response (left versus right), tactile probe latency (early versus late), and tactile probe location (left versus right). ERP mean amplitudes were analysed with repeated measures ANOVAs, and separate analyses were conducted for lateral anterior, central, and posterior sites. These analyses included the factors electrode site (F7/8 versus F3/4 versus FC5/6, for the anterior analysis, C3/4 versus T7/8 versus CP5/6, for the central analysis, and OL/R versus P3/4 versus P7/8, for the posterior analysis), cued response, hemisphere (left versus right), tactile probe latency, and tactile probe location. Importantly, the presence of ERP lateralisations sensitive to the side of a cued response will be revealed in these analyses by significant hemisphere × cued response interactions. Similar to our earlier studies of cued attentional orienting (cf., Eimer et al., 2002, 2003; Van Velzen et al., 2002), these analyses were based on mean amplitudes obtained between 350 and 600 ms (where the ADAN was previously observed), and between 600 and 900 ms after cue onset (where the LDAP component was found). An additional analysis was conducted for mean amplitudes between 900 and 1200 ms after cue onset, where the LRP was expected to emerge (see above).

ERPs triggered by the tactile probe stimuli were computed separately for early and late probes, relative to a 100 ms baseline prior to tactile stimulus onset, for all combinations of cued hand (left versus right) and stimulated hand (left versus right). ERP mean amplitudes were computed within latency windows centred on the peak amplitudes of early somatosensory ERP components (P90: 80–105 ms post-stimulus; N140: 130–160 ms post-stimulus). These mean amplitude values were analysed with repeated measures ANOVAs, separately for ERPs in response to early and late probes, and separately for midline electrodes (Fz, Cz), and for electrodes F3/4 and C3/4 contralateral and ipsilateral to the side of the stimulated hand, for the factors response preparation (tactile probe at cued versus uncued hand) and stimulation side (left versus right).

For all ERP analyses, Greenhouse-Geisser adjustments to the degrees of freedom were applied where appropriate. Manual response times (RTs) to Go stimuli were compared with paired *t*-tests for trials where tactile probes were presented to the cued hand, trials where probes were delivered to the opposite hand, and trials where probes were absent.

3. Results

3.1. Behavioural performance

Although tactile probes were entirely response-irrelevant, manual RTs to visual Go stimuli were affected by these probes. RTs were faster when tactile probes were presented to the cued hand (369 ms) relative to trials where probes were presented to the uncued hand (382 ms). RTs were slowest on trials without tactile stimulation (403 ms), presumably due to the absence of an unspecific alerting effect triggered when tactile events are presented during covert response preparation. Paired *t*-tests revealed that RTs differed significantly between all three types of trials (all $t\ (11) > 3.8$; all $p < .01$). False Alarms occurred on 10.9% of all Nogo trials. Participants failed to respond on 1.2% of all Go trials, and responded prematurely on 0.3% of these trials.

3.2. ERPs elicited during the response preparation interval following visual response cues

ERP modulations sensitive to the side of a cued unimanual response are first described informally before the results of statistical analyses are reported. Figs. 1 and 2 show ERPs elicited at lateral frontocentral electrodes (Fig. 1) and at lateral posterior electrodes (Fig. 2) for left and right visual response-hand selection cues on trials where tactile probes were present. Fig. 1 shows that an early visual response (N1) and a subsequent positivity elicited by the cue were followed by a sustained negativity (reflecting anticipation of the upcoming Go/Nogo signal and response). Somatosensory evoked potentials (SEPs) in response to early and late tactile probes ($\mathrm{SEP_e}$, $\mathrm{SEP_l}$) were superimposed on this sustained negativity. Importantly, an enhanced negativity contralateral to the side of the cued response appeared to be elicited about 350 after cue onset, analogous to the ADAN component observed in previous studies of spatial orienting. Towards the end of the response preparation interval, another enhanced negativity was elicited over the hemisphere contralateral to the side of the anticipated response. The latency of this lateralised negativity was similar to the effects observed in earlier studies of response precueing, and thus appears to reflect a LRP. Fig. 2 shows that at lateral posterior sites, early visual components triggered by the cue (P1, N1) were followed by an enhanced positivity contralateral to the side of the cued response. This lateralised effect started at about 600 ms after the onset of the response cue, similar to the LDAP component observed in previous studies of covert attentional orienting.

The difference waveforms shown in Fig. 3 further visualise the amplitudes and the time course of these lateralised ERP modulations elicited during covert response preparation for all lateral electrode pairs included in the present study. These waveforms were generated by first subtracting ERPs recorded during the preparation of a right-hand response from ERPs elicited during left-hand response preparation. To extract the lateralised portion of any differential response, difference waveforms obtained for right-hemisphere electrodes were then subtracted from the difference waveforms emerging at homologous electrodes over the left hemisphere. In the resulting double subtraction waveforms, a negativity contralateral to the side of a cued response is reflected by positive amplitude values (downward-going deflections), and a contralateral positivity is indicated by negative values (upward-going deflections). Fig. 3 shows difference waveforms obtained for anterior (top panel), central (middle panel), and posterior (bottom panel) electrode pairs.[1] An early anterior contralateral negativity (ADAN), starting about 350 after cue onset, was followed by a posterior contralateral positivity (LDAP) with an onset latency of about 500 ms, and by a contralateral negativity (LRP) starting about 900 ms after cue onset, which was most prominent over electrodes C3/4.

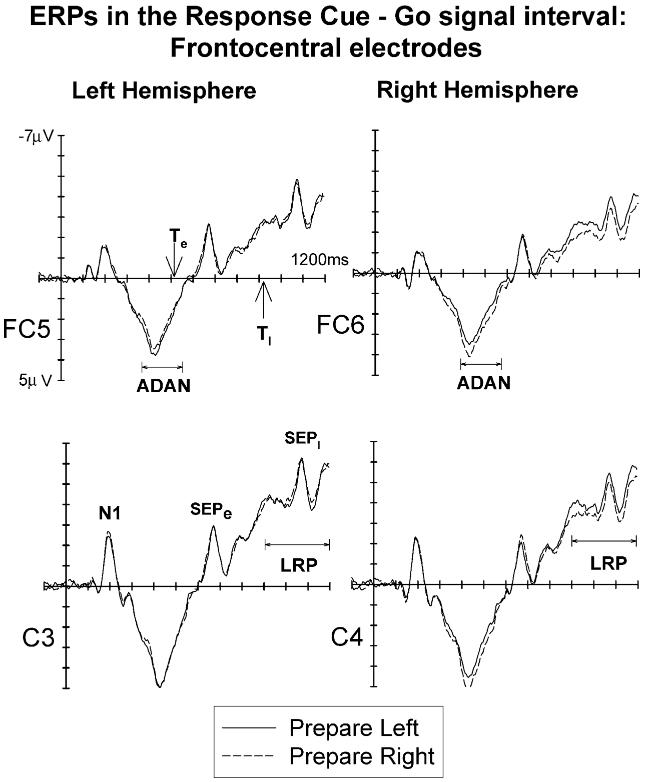

Fig. 1. Grand-averaged ERPs elicited during covert manual response preparation at frontocentral electrodes over the left hemisphere (FC5, C3) and over the right hemisphere (FC6, C4) in the 1200 ms interval following the onset of a visual response cue signalling an upcoming left-hand response (solid lines) or right-hand response (dashed lines). Waveforms are collapsed across all trials where tactile probes were delivered early (520 ms after cue onset) or late (920 ms after cue onset), as well as across trials where probes were delivered to the left or right hand. $\mathrm{T_e}$, $\mathrm{T_l}$: onset latencies of early and late tactile probes; $\mathrm{SEP_e}$, $\mathrm{SEP_l}$: somatosensory ERP responses to early and late tactile probes; ADAN: anterior directing attention negativity; LRP: lateralised readiness potential.

These informal observations were confirmed by statistical analyses. No significant ERP lateralisations sensitive to

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[1] These difference waveforms are included exclusively to simplify graphical presentation, and to highlight the effects revealed by the statistical analyses reported below, but not for formal statistics.

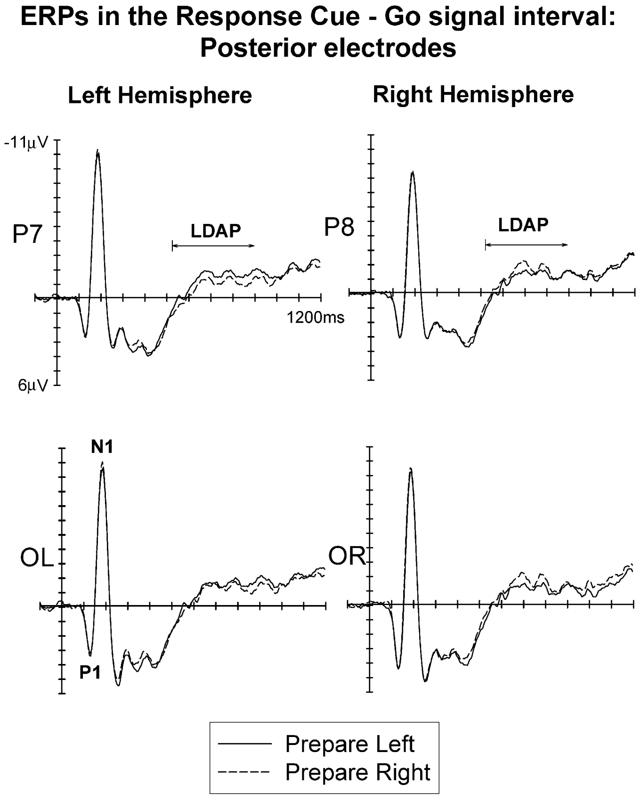

Fig. 2. Grand-averaged ERPs elicited during covert manual response preparation at posterior electrodes over the left hemisphere (P7, OL) and over the right hemisphere (P8, OR) in the 1200 ms interval following the onset of a visual response cue signalling an upcoming left-hand response (solid lines) or right-hand response (dashed lines). Waveforms are collapsed across all trials where tactile probes were delivered early or late and to the left or right hand. LDAP: late directing attention positivity.

the side of a cued response were present in the first 350 ms after cue onset. In the 350–600 ms interval, a significant hemisphere × cued response interaction was present at lateral anterior electrodes (F (1,11) = 6.6; $p < .03$), reflecting the ADAN component as shown in Figs. 1 and 3. No such interactions were present at lateral central and posterior electrodes. In the 600–900 ms interval, a hemisphere × cued response interaction was obtained at lateral posterior sites (F (1,11) = 17.1; $p < .001$), due to the presence of the LDAP component (see also Figs. 2 and 3). No hemisphere × cued response interaction was found for lateral anterior or central electrodes during this interval. In the 900–1200 ms interval, the hemisphere × cued response interaction was still significant at lateral posterior electrodes (F (1,11) = 5.7; $p < .04$), indicating that the posterior LDAP remained present throughout the covert response preparation interval (see also Fig. 3, bottom). In contrast, no overall significant hemisphere × cued response interactions were obtained at lateral anterior and central electrodes between 900 and 1200 ms. Follow-up analyses revealed that hemisphere × cued response interactions were significant only for the two electrode pairs closest to primary motor cortex (FC5/6 and C3/4; both F (1,11) > 6.2; both $p < .03$), as would be expected if the late contralateral negativity reflected an LRP.

3.3. Somatosensory ERPs elicited in response to early and late tactile probe stimuli

Figs. 4 and 5 show somatosensory ERPs in response to tactile probe stimuli delivered to the cued versus uncued hand at midline electrodes, for trials where probes were delivered early (520 ms after cue onset; Fig. 4), and late (920 ms after cue onset; Fig. 5) during the response preparation interval. Early somatosensory components (P90, N140) appear to be strongly affected by covert response preparation. When tactile probes were delivered early (Fig. 4), the N140 component was enhanced for tactile probes delivered to the cued index finger relative to probes delivered to the uncued finger. This was reflected in significant main effects of response preparation on N140 amplitudes (measured between 130 and 160 ms post-stimulus) at midline (F (1,11) = 7.7; $p < .02$), and ipsilateral electrodes (F (1,11) = 7.6; $p < .02$), and this effect approached significance at contralateral sites (F (1,11) = 3.8; $p < .08$). No significant effects of response preparation were present for the P90 component (measured between 80 and 105 ms post-stimulus) elicited by early probes (Fig. 4).

When probes were delivered late during the response preparation interval, the N140 component was again enhanced for probes delivered to the cued hand (Fig. 5). This was reflected in significant main effects of response preparation at midline sites (F (1,11) = 5.3; $p < .05$) and at contralateral electrodes (F (1, 11) = 5.6; $p < .04$), although this effect failed to reach significance at ipsilateral sites. In addition, and in contrast to the results obtained for early probes, ERPs to tactile stimuli delivered late during the response preparation interval also revealed a preparation-specific modulation of the earlier P90 component (see Fig. 5). P90 amplitudes were enhanced when late probes were presented to the cued hand relative to probes delivered to the uncued hand. Accordingly, significant main effects of response preparation were present at midline electrodes (F (1,11) = 5.7; $p < .04$) and at ipsilateral sites (F (1,11) = 7.4; $p < .02$), but not for contralateral electrodes.

4. Discussion

The present study used ERP measures to provide new evidence for the premotor theory of attention (Rizzolatti et al., 1994), which claims that attention and response processes are closely linked, because they are controlled by shared sensorymotor mechanisms. According to premotor theory, the activation of these control mechanisms during response preparation will trigger shifts of spatial attention. To investigate whether shifts of spatial attention are elicited during the covert preparation of simple unimanual responses, we recorded ERPs while participants were preparing to lift their left or right index finger (as indicated by a visual precue

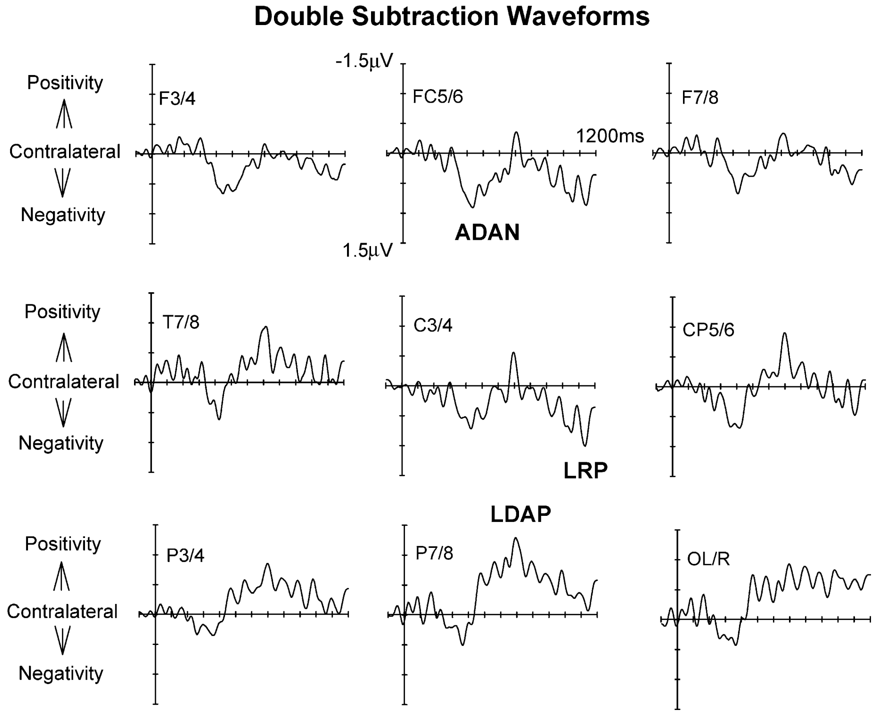

Fig. 3. Difference waveforms obtained at lateral anterior (top), lateral central (middle), and at lateral posterior (bottom) electrodes during covert response preparation. Enhanced negativities contralateral to the side of a cued response are reflected by positive values (downward deflections), and enhanced contralateral positivities are reflected by negative values (upward deflections). Three lateralised components (ADAN, LDAP, LRP) are elicited successively during the covert response preparation interval. See text for further details.

presented at the start of each trial) in response to a visual Go stimulus presented 1100 ms after cue onset. On a minority of trials, a Nogo stimulus was presented instead, and the prepared response had to be withheld. Task-irrelevant tactile probe stimuli that were presented during the covert response preparation interval to the left or right index finger had to be entirely ignored.

The presence of attentional shifts towards the side indicated by the response precues was substantiated in two different ways. First, we compared ERP waveforms elicited by

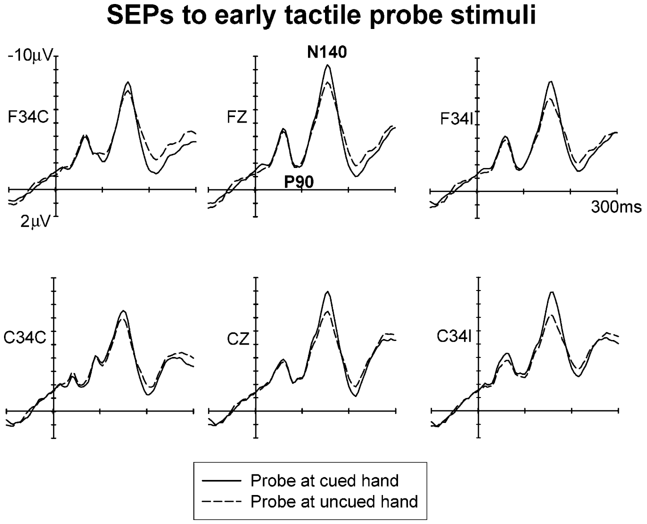

Fig. 4. Grand-averaged somatosensory ERPs elicited by ‘early’ tactile probe stimuli delivered 520 ms after the onset of the visual response-hand selection cue, in response to probes delivered to the cued index finger (solid lines) and to the uncued index finger (dashed lines). Waveforms are plotted relative to a 100 ms pre-stimulus baseline, and are shown for midline electrodes (Fz, Cz) as well as for frontocentral electrodes contralateral (C; left) and ipsilateral (I; right) to the stimulated hand.

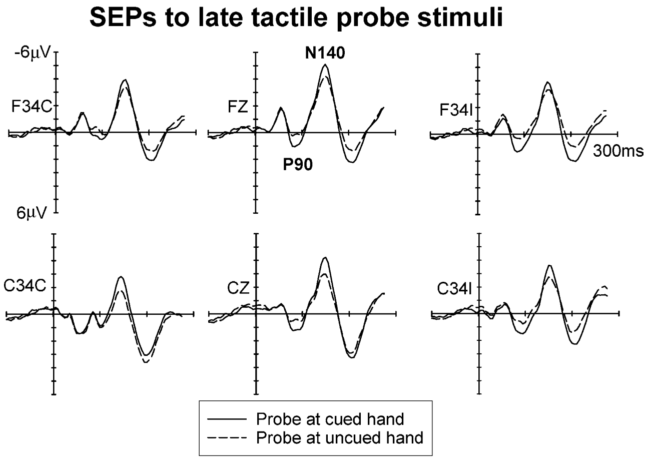

Fig. 5. Grand-averaged somatosensory ERPs elicited by ‘late’ tactile probe stimuli delivered 920 ms after the onset of the visual response-hand selection cue, in response to probes delivered to the cued index finger (solid lines) and to the uncued index finger (dashed lines). Waveforms are plotted relative to a 100 ms pre-stimulus baseline, and are shown for midline electrodes (Fz, Cz) as well as for frontocentral electrodes contralateral (C; left) and ipsilateral (I; right) to the stimulated hand.

cues signalling an upcoming left-hand versus right-hand response. If unimanual response preparation were linked to shifts of spatial attention, any preparation-induced lateralised ERP modulations should be similar to the effects observed in previous investigations where the direction of covert spatial attention shifts was explicitly manipulated (cf., Eimer et al., 2002; Harter et al., 1989). Second, we investigated whether somatosensory ERP components elicited by irrelevant tactile probe stimuli delivered during the covert preparation interval to the currently response-relevant hand would be enhanced relative to components triggered by tactile events presented to the uncued hand, analogous to attentional modulations of somatosensory ERPs observed in previous studies were endogenous tactile spatial attention was explicitly manipulated (cf., Eimer & Forster, 2003b; Michie et al., 1987).

Both analyses revealed unequivocal evidence that attentional orienting processes are in fact elicited during unimanual response preparation. The comparison of ERPs elicited during the covert unimanual preparation interval in response to left versus right response precues revealed a succession of lateralised ERP modulations. An initial negativity at anterior electrodes contralateral to the side of the cued response starting at about 350 ms post-stimulus was followed by an enhanced positivity over contralateral posterior electrodes, and a late contralateral negativity, which was more narrowly focused over lateral central electrodes C3/4. The first two of these lateralised components were very similar to the ADAN and LDAP effects observed previously in response to precues explicitly signalling the direction of a covert endogenous attentional shift (cf., Eimer et al., 2002; Nobre et al., 2000).[2] ADAN and LDAP have previously been interpreted as electrophysiological correlates of attentional processes involved in the control of spatial orienting, which are activated in anticipation of an expected task-relevant sensory stimulus at a specific location. In the present experiment, where covert unimanual response preparation was manipulated instead of spatial attention, participants were continuously monitoring central visual space for an upcoming visual Go or Nogo stimulus. This was done to ensure that visual attention would remain at fixation throughout the covert preparation interval. In spite of this difference, ADAN and LDAP components were clearly present in the current experiment. Moreover, their latencies and scalp distributions were strikingly similar to the ADAN and LDAP effects found in earlier ERP studies investigating covert spatial orienting (cf., Eimer et al., 2002; Nobre et al., 2000). In line with the predictions derived from the premotor theory, these similarities strongly suggest that attentional orienting processes are triggered during covert unimanual response preparation, and that these orienting processes may be equivalent to the processes elicited during instructed endogenous shifts of spatial attention.

The third lateralised component (an enhanced negativity elicited contralateral to the side of a cued response towards the end of the preparation interval) is very likely to represent the lateralised readiness component (LRP). LRPs have previously been observed in response precueing experiments at similar latencies, and have been interpreted as evidence for the partial activation of an anticipated response (Gehring et al., 1992; Gratton et al., 1990). In the present study, this effect only reached significance for lateral central electrodes close to primary motor cortex (C3/C4), which is line with the assumption that it reflects preparatory motor-related activation. In contrast, the earlier ADAN (which, like the LRP, also reflects a contralaterally enhanced negativity), was elicited maximally at lateral anterior sites (see Fig. 3).[3]

Analyses of somatosensory ERPs elicited by task-irrelevant tactile probes provided additional evidence for the hypothesis that the covert preparation of a unimanual response triggers concomitant shifts of attention towards the side of the effector involved in this response. The amplitude of early ERP components (P90, N140) was enhanced when probe stimuli were delivered to the response-relevant hand. P90 and N140 are modality-specific somatosensory ERP components, which are assumed to be generated in secondary somatosensory cortex (Frot & Mauguière, 1999; Frot, Rambaud, Guénot, & Mauguière, 1999). Thus, the present results demonstrate that spatially selective modulations of early sensory-perceptual stages in the processing of tactile information are induced when simple unimanual responses are covertly prepared. The amplitude modulations shown in Figs. 4 and 5 are very similar to the modulations found in previous ERP studies where tactile-spatial attention was explicitly manipulated (Eimer & Forster, 2003a, 2003b; Michie et al., 1987), thus supporting the hypothesis that covert response preparation results in concomitant shifts of spatial attention.

It is notable that systematic effects of covert response preparation on the N140 component were observed for tactile probes presented early during the response preparation interval (580 ms prior to the Go signal). This demonstrates that, analogous to the effects of saccade programming on visual attention (Deubel & Schneider, 1996; Hoffman &

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[2] However, the size of the ADAN observed in the present study was smaller than the ADAN effects observed in previous ERP studies where cues indicated the side of a covert attentional shift (e.g., Eimer et al., 2003; Nobre et al., 2002), rather than the side of an upcoming unimanual response. This difference, which needs to be evaluated in future experiments, could suggest that relative to explicitly cued covert attention shifts, anterior attentional control mechanisms are activated less consistently across trials, or are less well time-locked to the cue, when unimanual responses are prepared in the absence of explicit instructions to shift attention.

[3] It should be noted that these lateralised effects are partially consistent with results previously reported by Van der Lubbe et al. (2000). These authors identified six lateralised components elicited during the covert preparation of saccades or finger movements. Early activations over posterior sites (corresponding to three of their components) are likely to reflect the processing of non-symmetrical (i.e., arrow) cues rather than processes linked to response preparation or shifts of attention (see Van Velzen & Eimer, 2003, for more details). However, two other components (a frontal contralateral negativity and an posterior contralateral negativity) observed by Van der Lubbe et al. (2000) may be analogous to the ADAN and LDAP effects found in the present experiment.

Subramaniam, 1995; Irwin & Gordon, 1998), shifts of tactile attention towards the location of a prepared response are not time-locked to the onset of this response, but already occur well in advance of response execution. However, effects of response preparation on the earlier P90 component were only present when probes were presented late (180 before the onset of the Go signal). This difference could indicate that, as unimanual response activation builds up during the preparation interval, attentional modulations come to affect earlier stages of somatosensory processing. It should also be noted that the present study found no evidence for any suppression of tactile processing for stimuli delivered to the hand involved in an upcoming response (Starr & Cohen, 1985). It is likely that such inhibitory effects may only emerge immediately before response execution (cf., Williams, Shenasa, & Chapman, 1998).

5. Conclusions

In line with the premotor theory of attention (Rizzolatti et al., 1994), the current findings demonstrate for the first time strong links between response preparation and spatial attention outside the oculomotor domain, suggesting that the activation of sensorymotor control systems responsible for the programming of manual responses triggers covert shifts of attention towards the side of the effector involved in the execution of these responses. While these links are consistent with the assumption of the premotor theory of attention that spatial orienting and response programming are based on shared sensorymotor control mechanisms, they are also compatible with the claim that attention and response preparation are mediated by anatomically distinct, but causally closely connected neural networks.

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