Frontoparietal Control of Spatial Attention and Motor Intention in Human EEG

Peter Praamstra,1,2 Luc Boutsen,1 and Glyn W. Humphreys1
1Behavioural Brain Sciences Centre and 2Department of Clinical Neurology, Queen Elizabeth Hospital, University of Birmingham, Birmingham, United Kingdom

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Praamstra, Peter, Luc Boutsen, and Glyn W. Humphreys, Frontoparietal control of spatial attention and motor intention in human EEG. J Neurophysiol 94: 764–774, 2005. First published March 2, 2005; doi:10.1152/jn.01052.2004. Relations between spatial attention and motor intention were investigated by means of an EEG potential elicited by shifting attention to a location in space as well as by the selection of a hand for responding. High-density recordings traced this potential to a common frontoparietal network activated by attentional orienting and by response selection. Within this network, parietal and frontal cortex were activated sequentially, followed by an anterior-to-posterior migration of activity culminating in the lateral occipital cortex. Based on temporal and polarity information provided by EEG, we hypothesize that the frontoparietal activation, evoked by directional information, updates a task-defined preparatory state by deselecting or inhibiting the behavioral option competing with the cued response side or the cued direction of attention. These results from human EEG demonstrate a direct EEG manifestation of the frontoparietal attention network previously identified in functional imaging. EEG reveals the time-course of activation within this network and elucidates the generation and function of associated directing-attention EEG potentials. The results emphasize transient activation and a decision-related function of the frontoparietal attention network, contrasting with the sustained preparatory activation that is commonly inferred from neuroimaging.

INTRODUCTION

Research on visuospatial attention generally distinguishes between processes involved in directing attention to a location in space and the selective facilitation of sensory input originating from that location (Corbetta and Shulman 2002; Kastner and Ungerleider 2000). It has long been recognized that the allocation of attention in space may involve activation of brain structures for motor control, even when attention is directed covertly without moving the eyes (Klein 1980; Rizzolatti et al. 1987). Brain imaging studies have indeed established considerable overlap between structures involved in control of spatial attention and those responsible for eye movements (Corbetta 1998; Nobre et al. 2000a; Perry and Zeki 2000). Motor activation engaged by the control of spatial attention also extends to domains other than the oculomotor system (Chelazzi and Corbetta 2000; Sheliga et al. 1997; Tipper et al. 1998). Here we studied the relation between spatial attention and motor intention for hand movements using high-density EEG.

The allocation of attention in space is often studied using a paradigm in which attention is cued on a trial-by-trial basis toward left or right hemi-space in anticipation of a target stimulus (Posner et al. 1980). Shifts of attention from fixation to a cued location produce a number of different event-related potential (ERP) effects in the time elapsing between presentation of cue and target (Harter et al. 1989; Hopf and Mangun 2000; Nobre et al. 2000b; van Velzen and Eimer 2003). The most consistent ERP effects occur over frontocentral and occipitotemporal areas in the form of voltage differences between the hemispheres ipsilateral and contralateral to the attended hemisphere. These effects are labeled anterior directing-attention negativity (ADAN) and late directing-attention positivity (LDAP), respectively. Previous work has shown that these directing-attention potentials reflect supramodal control of spatial attention, because they occur independently of the sensory modality through which attention is tested (Eimer et al. 2002). We studied here whether the control operations reflected in the directing-attention potentials are supramodal in a second sense, namely whether they control perception and action. The directimg-attention ADAN component provides a possible means to address this question, because previous work suggests that it can be elicited by shifting attention to a location in space as well as by the selection of a hand for responding (Eimer 1995; Verleger et al. 2000). What functional process is responsible for the movement and attention-related properties of the ADAN is not clear, however. Using high-density EEG, we orthogonally varied spatial attention and response information provided by a directional cue, to evaluate the overlap in their associated brain electrical activities and to identify a common functional process.

A further goal was to clarify the generation of the directing-attention ERPs. Imaging studies of spatial attention have shown a consistent pattern of bilateral parietal and frontal activation, often referred to as the frontoparietal attention network (Corbetta and Shulman 2002; Gitelman et al. 1999). Like the directing-attention ADAN, this attention network may not only be involved in the control of attention, but also in response selection (Corbetta and Shulman 2002). Possible relations between the directing-attention ERPs and this frontoparietal network have been suggested (Hopf and Mangun 2000; Macaluso et al. 2003; Nobre et al. 2000b), but it is not known in detail how they are related. It is unexplained, for instance, how the bilateral frontoparietal network, which is relatively insensitive to the direction of attention shifts (Corbetta and Shulman 2002; Kastner and Ungerleider 2000), can be responsible for directing-attention potentials with a lateralization dependent on the direction of attention. This study used...
higher spatial resolution than previous EEG studies and enabled a reconstruction that resolved bilateral frontal, parietal, and occipital activations related to the directing-attention EEG potentials.

METHODS

Participants

Twelve participants (7 women; age, 28 ± 6 yr), of whom 11 were right-handed, took part in the experiment. All had normal or corrected-to-normal vision. Informed consent was obtained, and the study was approved by the department’s ethical review board.

Procedures and stimuli

The experiment was comprised of four attention/response precueing tasks, each consisting of two blocks of 100 trials preceded by a practice block of 32 trials. The trial structure was the same in each task (Fig. 1). Throughout each trial, two square boxes were displayed in the left and right lower quadrants and target stimuli appeared in these boxes. At the start of each trial, a centrally presented directional cue (left or right pointing arrows) or a nondirectional cue (overlapping arrows pointing in opposite directions) was presented. The directional cue pointed to the left or right box with equal probability. After a cue-target interval of 1000 ms, a target and a filler stimulus appeared in the two boxes. Participants had to make a manual response to the target stimulus as quickly and accurately as possible, according to instructions set out for each task. The four tasks differed in the directional information provided by the cue. The order of the tasks was counterbalanced across participants.

ATTENTION TASK. The arrow cue directed covert attention to the left or right target location, where a differently shaped arrow (composed of 5 horizontal bars; Fig. 1) appeared as imperative signal instructing for a left or right hand response with equal probability. In this task, the cue directs attention to one side but response selection is contingent on the later presentation of the imperative stimulus. The cue was always valid.

ATTENTION-MOTOR TASK. The same arrow cue as in the previous task instructed to attend to the left or to the right target location and to prepare a manual response on the same side. Maintenance of covert spatial attention to the cued side was ensured by including 10 randomly occurring Nogo trials, which were signaled by a vertical orientation of the stimulus appearing in the box in the cued hemifield. In this task, the cue both directs attention to a critical location and it allows response selection and preparation to take place.

MOTOR TASK. The same arrow cue as in the previous tasks instructed here to select and prepare a left or right hand response. There was no need to direct spatial attention, as the imperative stimulus was identical on both sides and provided only the signal to initiate the prepared response.

NEUTRAL TASK. A nondirectional cue was presented by overlaying left and right pointing arrows. The subsequent target stimulus appeared (with equal probability) in the left or right hemifield and consisted of an equiprobable left or right pointing arrow, requiring a left or right hand response.

The experiment was run in a normally illuminated room. Stimuli were presented on an SVGA monitor. Participants were seated comfortably in an armchair with their eyes 100 cm from the monitor. Response keys were attached to the armrests of the chair and subjects rested their index fingers on the keys. The stimuli were presented in white on a gray background. The brackets surrounding the cue, enclosing a square of 0.5 × 0.5° of visual angle, were displayed permanently and served as fixation signal. The vertical separation between the positions of cue and imperative stimulus was 1° (center to center). The horizontal separation between the boxes (measuring 0.85° × 0.85°) was 2.3° of visual angle. Cues and target stimuli were displayed for 100 ms.

EEG recording and data processing

EEG was recorded continuously with Ag/AgCl electrodes from 128 scalp electrodes relative to an (off-line) averaged left and right ear reference. The electrodes were placed according to the 10–5 electrode system (Oostenveld and Praamstra 2001), using a nylon electrode cap. Eye movements were monitored by bipolar horizontal and vertical EOG derivations. EEG and electro-oculogram (EOG) signals were amplified with a band-pass of 0–128 Hz by BioSemi Active-Two amplifiers and sampled at 512 Hz. The continuous EEG recordings were off-line segmented in epochs from 100 ms before cue-onset to 1,000 ms after target-onset. Individual trials containing eye movement artifacts were rejected before averaging. Of primary interest were movement-related and attention-related EEG potentials developing between cue and target presentation, superimposed on the contingent negative variation (CNV). Evaluation of the lateralized topography of these potentials was performed by deriving lateralized event-related potentials (L-ERPs), i.e., the movement-related lateralized readiness potential (LRP) and the attention-related ADAN and LDAP. The derivation involved computation of difference potentials between homologous electrodes contra and ipsilateral to the side of movement or the side of attention. Subsequently, difference waveforms associated with left and right cue conditions were averaged to obtain movement and attention-related L-ERPs. The amplitude of the ADAN was quantified from pooled electrode pairs C1/2, C3/4, FC1/2, FC3/4, and FCC3h/4h as the mean amplitude between 325 and 425 ms. The amplitude of the LDAP was measured from pooled electrode pairs P5/6, P7/8, P07/8, Po5h/6h, and PoP5h/6h as the mean amplitude between 500 and 600 ms. Further analyses on data not involving contralateral-ipsilateral subtractions are specified in RESULTS.

Analyses

Performance was evaluated in terms of reaction time and accuracy. Reaction times were measured from the onset of the target until the response. Reaction times were compared between tasks, while separate analyses within tasks evaluated spatial congruity effects between cue and targets (Attention condition), and between spatial location of target and responses (Neutral condition). Data were evaluated with
TABLE 1.  Reaction times and error rates for each of the tasks

<table>
<thead>
<tr>
<th>Task</th>
<th>Cue Direction/Target Location</th>
<th>Target Direction/Response Side</th>
<th>RT, ms</th>
<th>Percent Errors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attention</td>
<td>Cue left</td>
<td>Left</td>
<td>520 ± 22</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>Cue left</td>
<td>Right</td>
<td>528 ± 27</td>
<td>4.0</td>
</tr>
<tr>
<td></td>
<td>Cue right</td>
<td>Left</td>
<td>534 ± 26</td>
<td>5.3</td>
</tr>
<tr>
<td></td>
<td>Cue right</td>
<td>Right</td>
<td>487 ± 20</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td>Target left</td>
<td>Left</td>
<td>515 ± 23</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Target right</td>
<td>Right</td>
<td>537 ± 20</td>
<td>7.0</td>
</tr>
<tr>
<td></td>
<td>Target left</td>
<td>Right</td>
<td>545 ± 20</td>
<td>4.7</td>
</tr>
<tr>
<td></td>
<td>Target right</td>
<td>Left</td>
<td>497 ± 18</td>
<td>1.5</td>
</tr>
<tr>
<td>Attention-motor</td>
<td>Cue left</td>
<td>Left</td>
<td>472 ± 21</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>Cue right</td>
<td>Right</td>
<td>458 ± 20</td>
<td>1.4</td>
</tr>
<tr>
<td>Motor</td>
<td>Cue left</td>
<td>Left</td>
<td>368 ± 34</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>Cue right</td>
<td>Right</td>
<td>363 ± 33</td>
<td>3.7</td>
</tr>
</tbody>
</table>

Values are means ± SE.

Analyses within tasks showed for the Attention task that responses were faster when the attended side and response side were the same than when they were different (interaction of cue direction and response side; $F(1,11) = 5.53, P < 0.05$). This congruency effect was also expressed in error rates ($F(1,11) = 8.0, P < 0.05$). Stimulus-response congruency effects were also obtained in the Neutral task, for response times ($F(1,11) = 26.3, P < 0.001$) and errors ($F(1,11) = 32.1, P < 0.001$). Together, the behavioral data show low error scores and reaction time effects consistent with the different task demands, indicating that participants complied with the instructions and deployed the directional information to improve their performance. Note, however, the curiously similar performance in the Attention and Neutral tasks.  

ADAN

In the three tasks where the cue provided directional information, transient lateralized activity developed over the frontocentral scalp regions. The lateralization was isolated by means of contralateral-ipsilateral subtractions (see METHODS), yielding the ADAN with a peak amplitude around 400 ms. After a return to baseline, the ADAN was followed by a more sustained negative wave (foreperiod LRP; cf. Leuthold and

1Although it seems curious that the Attention task and the Neutral task produced similar reaction times and spatial stimulus-response congruency effects, this is in agreement with previous work (Proctor et al. 1992; Verfaellie et al. 1988; Wascher and Wolber 2004). To verify (independent from the directing-attention EEG potentials) that lateralized spatial attention was engaged in the first but not the second task, we studied interhemispheric amplitude differences of visual responses evoked by the targets. Analyses of the P1 and N1 amplitudes did not distinguish between the two tasks. This may have been due to the fact that target stimuli were accompanied by filler stimuli in the opposite hemifield, whereas previous work on the modulation of visual-evoked responses by spatial attention has used unilateral stimuli, comparing responses to validly and invalidly cued targets (e.g., Mangun and Hillyard 1991). However, as a result of the bilateral stimulus display with target and filler stimuli left and right from fixation, an N2pc was elicited that separated the Attention and the Neutral tasks. The N2pc reflects an attentional selection process invoked to suppress competing information. The demands on this process are higher in a task that requires target localization, as in our Neutral task, than in a task where target location is known, as in our Attention task (cf. Luck et al. 1997). Consequently, the N2pc amplitude should be higher in the Neutral task. This prediction was borne out with a significant amplitude difference between the tasks over the occipital scalp ($F(1,11) = 12.73, P < 0.01$), as quantified by the mean amplitude between 200 and 300 ms in pooled electrode pairs PO5h/6h, PO3h/4h, PPO3h/4h, and O1/O2. The N2pc amplitude difference supports the assumption that subjects allocated spatial attention to the cued hemifield in the Attention task.
The Attention, Attention-Motor, and Motor tasks were each evaluated from five pooled frontocentral electrodes and was significantly different between tasks \(F(3,33) = 11.7, P < 0.001\). Posthoc comparisons confirmed that the ADANs for the Attention, Attention-Motor, and Motor tasks were each significantly different from the Neutral task \(t(11) = 3.4, 4.9, 4.6, P < 0.05\). The amplitude differences of the Attention-Motor and Motor task ADAN, relative to the Attention task ADAN, just failed the Bonferroni adjusted significance threshold \(t(11) = 2.9, 2.4\). The distribution was assessed from a 3 \(\times\) 4 grid of 12 electrodes overlying the frontocentral scalp by an ANOVA including the grid axes (medial-lateral and anterior-posterior) as independent factors. This analysis did not reveal any topographic difference between the Attention, Attention-Motor, and Motor tasks on the anterior-posterior axis \(F(6,66) = 1.09, P = 0.38\) or on the medial-lateral axis \(F(4,44) = 1.32, P = 0.28\).

The topography of the ADAN differed from the distribution of the movement execution-related LRP developing after the imperative signal. On the same 3 \(\times\) 4 grid of electrodes, the ADAN had a more anterior maximum and a flatter distribution than the LRP, producing differences on the anterior-posterior axis \(F(2,11,23,20) = 6.22, P = 0.01\) and the medial-lateral axis \(F(2,22) = 5.8, P = 0.01\). Together, these results confirm the attention and response-related properties of the ADAN, being elicited both by shifts of spatial attention and by the selection of a response (Eimer 1995; Verleger et al. 2000). They also support that the ADAN can be topographically differentiated from response execution-related motor cortex activation (Verleger et al. 2000). The more anterior distribution points to a generation just anterior to the primary motor cortex, i.e., the lateral premotor cortex.

**LDAP**

In the time frame between 400 and 700 ms after cue presentation, a lateralization of positive polarity developed over occipitotemporal regions contralateral to the direction of attention, peaking at \(\sim 550\) ms. Like the lateralization over frontocentral areas, this activity was analyzed by means of contralateral-ipsilateral subtractions and evaluated from five pooled occipitotemporal electrodes. The latency and distribution conformed to what has previously been designated as LDAP. Like the anterior lateralization, the LDAP was only present for the conditions where the cue provided directional information, i.e., the direction of spatial attention (Attention and Attention-Motor tasks) and/or the response side (Motor and Attention-Motor tasks), yielding a main effect of Task \(F(2,49,27,38) = 3.19, P < 0.05\). In posthoc tests, only the Motor task was significantly different from the Neutral task \(t(11) = 3.50, P < 0.05\). A separate analysis established that there was no difference in LDAP amplitude between the three tasks where directional information was provided \(F(2,22) < 1\). The combined LDAP from these tasks differed significantly from the Neutral task, where no LDAP was apparent \(F(1,11) = 6.16, P < 0.05\). These analyses suggest that not only the ADAN, but also the LDAP can be elicited by the selection of the side of a manual response, as well as by attention shifts. Figure 3 shows the spatial and temporal relationship of the ADAN and the LDAP.

**ERPs to directionally informative and noninformative cues**

The lateralized ADAN and LDAP are derived by subtracting left and right cue conditions, thus subtracting out nonlateralized activity. However, the latter activity may nonetheless contain activity associated with the allocation of spatial attention and with response selection. Hence, it is mandatory to complement the analysis of lateralized ERPs with an evaluation of the ERPs from which they are derived. Figure 4 shows these ERPs from parietal electrodes. Of interest is the amplitude modulation in the time frame of the P300 between 250 and 500 ms, where the Attention-Motor, Motor, and Attention tasks show a P300, whereas the Neutral task shows a negative-going deflection. The timing and amplitude relations between tasks are the same as shown in the ADAN. A closer evaluation of the ERPs in this time window could therefore reveal features of brain activation associated with the control of spatial attention and motor intention that are related to but not captured in the ADAN.

ERPs in the P300 time frame showed scalp topographies with four activation maxima in bilateral frontal and parietal areas for the Attention, the Attention-Motor, and the Motor tasks. Subtraction of the waveforms of the Neutral task from each of the other task conditions was performed separately for left and right cue conditions. This subtraction removed residual
stimulus-related activity, thus producing a more selective topography of the cue-related activity, as shown in Fig. 4. Activations clustered around electrodes FFC3h and FFC4h (left and right frontal) and CPP3h and CPP4h (left and right parietal). The same characteristic topography with bilateral frontal and parietal activation was found when the Attention condition, instead of the Neutral condition, was subtracted from the higher amplitude Attention-Motor or the Motor condition. This confirmed that the frontoparietal activation was associated with the processing of a directional cue and did not depend on subtraction of the Neutral condition.

Differences in distribution of the bilateral parietal and frontal activation between the Attention, Attention-Motor, and Motor tasks were assessed from two rectangular $3 \times 5$ electrode grids overlying the left and right hemisphere activations (see Fig. 4). The analysis was performed on the mean amplitudes in a 50-ms time window from 375 to 425 ms, with the factors Task (3), Direction (2), Hemisphere (2), Anterior-posterior axis (5), and Medial-lateral axis (3). A main effect of Task \( F(2,22) = 3.63, P < 0.05 \) was explained by higher amplitudes for the Attention-Motor and Motor tasks than for the Attention task. Task did not interact with any other factor, indicating that there was no difference in the activation distribution between tasks. While there was no main effect of Hemisphere, activation was lateralized to the hemisphere ipsilateral to the direction of attention or motor preparation [interaction Direction by Hemisphere \( F(1,11) = 21.0, P < 0.001 \)]. In the 375- to 425-ms window analyzed here, this lateralization to the ipsilateral hemisphere involved only the frontal electrodes, as activity at parietal electrodes was highest over the left hemisphere after both left and right cues [interaction Direction by Hemisphere by Anterior-posterior axis; \( F(3,11,34,19) = 14.81, P < 0.001 \)]. On the medial-lateral axis, activation had a distinct maximum at the second of three rows of electrodes counted from the midline \( F(2,22) = 10.31, P < 0.01 \). Together, these analyses show, first, that coincident in time with the ADAN there is bilateral frontoparietal activation represented in the time window of the P300 event-related potential. This activation is missed when analyses are confined to subtractions of left and right cue conditions. Second, that the ADAN represents a modulation of the frontal activation within this network.

Dipole source analysis

The bilateral frontoparietal activation represents a prima facie plausible EEG manifestation of the frontoparietal attention network, given its characteristic distribution and antecedent conditions. We applied dipole source analysis to study the underlying sources, using a dataset averaged across subjects...
and tasks. Based on the voltage and current source density (CSD) topography, the activity seems to be generated by four radially oriented dipoles, localized in left and right frontal and parietal cortex. However, due to the shallow topography over dorsal scalp regions, in combination with a steep voltage gradient over lower regions (see Fig. 4), dipoles adopted locations in inferior frontal and temporal areas, assuming a tangential orientation. This modeling outcome was rejected as physiologically implausible.

Subsequently, dipole source analysis was performed on the lateralized potentials, i.e., the ADAN peaking at ~400 ms in frontocentral areas and the LDAP peaking at ~550 ms in the occipitotemporal region. Inverse modeling of these potentials is facilitated by the fact that symmetrical activity is subtracted out. To enable dipole source analysis of the lateralized potentials, they were duplicated over both hemispheres, with inverted polarity, and analyzed with anti-symmetrical dipole pairs (Praamstra et al. 1996b). Localization was performed with two regional source pairs, which were subsequently reduced to dipole sources. Sources were fitted to locations in the frontal and occipitotemporal region, explaining the data in the interval from 300 to 700 ms with a goodness-of-fit >90%. The frontal dipole pair, explaining the ADAN, was localized in the premotor cortex (X = ±33, Y = −7, Z = 54), as shown in Fig. 5. The premotor cortex localization corresponds well with the frontal activation of the frontoparietal attention network identified in imaging studies (e.g., Gitelman et al. 1999; Hopfinger et al. 2000; Kastner et al. 1999; Macaluso et al. 2003). The posterior LDAP was explained by a dipole pair localized to the middle occipital gyrus (X = ±49, Y = −67, Z = −4). This region is not within the frontoparietal network, but is nonetheless consistently activated by endogenous cues for spatial attention (Gitelman et al. 1999; Hopfinger et al. 2000; Macaluso et al. 2003).

Sequential topographies of frontoparietal activation

Dipole source analysis mapped ADAN and LDAP onto structures known to be activated during endogenous shifts of spatial attention. It left the parietal activation, suggested in Fig. 4, unaccounted for, as it was masked by the stronger lateralization of the frontal foci. We attempted to clarify the parietal activation with the help of sequential topographies. Subtractions of the directional cueing conditions minus the neutral condition were analyzed over six consecutive 25-ms intervals between 300 and 450 ms, with the left and right frontal and parietal activations quantified by pooling electrodes F1, F3, FC3, FC1, and FFC3h for the left frontal activation and their opposite hemisphere homologues for the right frontal activation. Similarly, the left and right parietal activations were isolated in electrode pools CP1, CP3, P1, and CPP3h and their right hemisphere homologues (Fig. 6). Activation at 300 ms shows parietal activation of positive polarity with maximum amplitude over the hemisphere ipsilateral to the direction of attention. The activation progressed from parietal to ipsilateral frontal cortex, reflected in a Direction by Hemisphere by Region interaction. That is, in each of the six windows significant Direction by Hemisphere interactions were obtained [F(1,11) = 24.2, 19.6, 14.1, 27.5, 31.6, 5.6; P < 0.05]. This direction-dependent hemispheric asymmetry became more pronounced after the activation maximum moved from parietal to frontal in the 350- to 375-ms window, yielding the three-way Direction by Hemisphere by Region interaction in the windows between 350 and 450 ms [F(1,11) = 6.55, 19.97, 18.44, 37.72; P < 0.05]. What further contributed to this three-way interaction was that parietal activation ipsilateral to the cue direction moved early to the contralateral hemisphere for the right cue condition (~350 ms), but only much later for the left cue condition (~425 ms). Finally, in each of the three windows between 375 and 450 ms, there was a significant main effect of Task [F(2,22) = 5.2, 3.63, 3.65; P < 0.05]. However, none of the interactions involving Task were significant, indicating that the effect represented a mere amplitude difference between the Attention condition and the Motor and Attention-Motor conditions.

Figure 7 extends the sequential topographies to earlier and later time windows. Topographies preceding the time window of the directing-attention potentials were inspected...
to evaluate whether the ipsilateral predominance of the frontoparietal activation was perhaps preceded by activation contralateral to the direction of the cue. Interestingly, this search revealed that the parietal activation emerged from a right parietal focus, irrespective of the direction of attention/motor preparation (Fig. 7A). This activation started around 225 ms and developed through a symmetrical stage, around 275 ms, to the ipsilaterally predominant parietal activation at 300 ms. The initial right hemisphere dominance was not captured by analyses on the same parietal electrode pools as above. Analyses on an adjacent more posterolateral electrode group (P4, P6, PO8, PO6h, PPO6h vs. left hemisphere homologues) yielded a significant asymmetry in the time window between 240 and 260 ms $[F(1,11) = 5.52, \; p < 0.05]$. There was no effect of Task ($F < 1$) or an interaction of Hemisphere by Task ($F < 1$).

Figure 6 showed how between 300 and 450 ms the parietal activation reverses from an initial ipsilateral to a later contralateral predominance. Figure 7B shows how these contralateral activation foci then descend to the occipitotemporal cortex (around electrodes PO7 and PO8) between 450 and 550 ms. The latency and the distribution of this activation correspond to the LDAP in lateralized potentials. Taken together, the analyses of sequential topographies of frontoparietal activation show that directional cues evoke distinct left and right hemisphere parietal activation. In addition, both the frontal ADAN and the occipitotemporal LDAP are preceded by parietal activation that subsequently moves to frontal and occipitotemporal locations, respectively.

**DISCUSSION**

The results of this study map in considerable detail how the directing-attention EEG potentials arise from bilateral frontoparietal activations and related occipitotemporal activation. This establishes a link to the frontoparietal attention network delineated by functional neuroimaging (Corbetta 1998; Gitelman et al. 1999; Hopfinger et al. 2000; Kastner et al. 1999; Macaluso et al. 2003). The proposed relation elucidates the hitherto largely ignored (but see Verleger et al. 2000) sensitivity of the ADAN to manual response selection. We first discuss the EEG manifestations of the frontoparietal attention network, outlining the time-course.
of activation in parietal and frontal cortex. We then discuss how the EEG evidence reflects on frontoparietal involvement in spatial attention and motor intention.

**Directing-attention EEG potentials and the frontoparietal attention network**

Previous work on the directing-attention EEG potentials has proposed a relation between these potentials and frontoparietal structures known to be involved in spatial attention (Eimer et al. 2002; Hopf and Mangun 2000; Nobre et al. 2000b). For the ADAN, suggested origins include lateral prefrontal cortex and lateral and medial premotor cortex. For the LDAP, they include posterior parietal cortex and ventral occipital cortex. Based on the present results, obtained with a higher electrode density, the lateral premotor cortex and the lateral occipital cortex are the most likely origins for the ADAN and the LDAP, respectively. In addition to more accurate localization, the main advance of the present study is the identification of a direct EEG manifestation of the frontoparietal network, yielding information beyond that provided by ADAN and LDAP. The time-course of attention-related brain activation is especially revealed in greater detail, showing a more complex pattern than simple anterior-to-posterior (Eimer et al. 2002) or posterior-to-anterior (Nobre et al. 2000b) progression of activation inferred from earlier EEG studies. Bilateral frontoparietal activation is manifest in EEG between ~300 and 450 ms, with an initial maximum at ipsilateral parietal sites that subsequently moves to the ipsilateral premotor cortex. Concurrent with that progression, the balance of activation between left and right parietal cortex reverses and the contralateral parietal activation descends to lateral occipitotemporal sites to generate the LDAP. Interestingly, in view of the important role of the right hemisphere in spatial attention inferred from spatial neglect after right hemisphere stroke, the bilateral frontoparietal activation is preceded by initial right hemisphere parietal activation at a latency as early as 250 ms.

The LDAP is not generated by structures partaking in the frontoparietal attention network, but it shares antecedent conditions with the ADAN, being evoked by spatial attention shifts (Eimer et al. 2002; Harter et al. 1989; Hopf and Mangun 2000), the preparation of saccadic eye movements (Verleger et al. 2000), and selection of the side of a manual response (these data). The origin in the lateral occipital cortex, suggested here, fits well with activation distributions commonly found in imaging studies of spatial attention (Gitelman et al. 1999; Hopfinger et al. 2000; Macaluso et al. 2003). The most articulate interpretation of lateral occipital activation in these imaging studies is that it reflects inferred movement of the attentional focus across the visual scene (Gitelman et al. 1999). Our finding that the LDAP can be evoked by manual response selection without an attention shift indicates a more general function. An interesting speculation is that the lateral occipital cortex activations and the LDAP reflect activation of the “extrastriate body area,” which is hypothesized to integrate visual, spatial attention, and motor signals for the dynamic updating of the observer’s body representation (Astafiev et al. 2004). Astafiev et al. considered this process related to the updating of visual space for eye and hand movements that takes place in the posterior parietal cortex (Duhamel et al. 1992). Our sequential mapping data reproduce a sequence of activation that supports this view (Astafiev et al. 2004). That is, the frontal activation presumably involved in the execution of attention shifts is followed by parietal activation involved in the remapping of visual space, which in turn, is followed by the lateral occipital activation related to the updating of the agent’s body representation. Explanation of the LDAP as activation of the extrastriate body area would accommodate the hitherto not well-understood observation that the LDAP is also elicited in anticipation of nonvisual stimuli. Based on the notion that the LDAP reflects preparatory activation of visual areas (Harter et al. 1989), this was previously explained by a presumed dominance of the visual modality in multimodal spatial attention (Eimer et al. 2002).

As for the ADAN, previous work has documented a frontal distribution (Eimer et al. 2002; Hopf and Mangun 2000) and tight time-locking to the directional cue preceding it (van Velzen et al. 2002). These characteristics have been regarded as evidence that the ADAN reflects the voluntary control of attention shifts. The present data reproduce an earlier observation that the ADAN can also be elicited by the selection of a manual response, when no attention shift is required (Verleger et al. 2000). Attention shifts and manual response selection might both involve covert motor preparation, albeit of different, though adjacent, cortical areas, i.e., the frontal eye fields and the hand (pre)motor cortex, respectively. However, this reconstruction must be rejected on two accounts. First preparatory cortical potentials related to hand movement are reflected in scalp-recorded EEG lateralizations, but no such lateralization is found for cortical potentials related to eye movement (van ’t Ent and Apkarian 1998; Wauschkuhn et al. 1997). Second, a novel and surprising finding of this study is that the ADAN seems not due to brain electrical activity of negative polarity contralateral to the direction of attention or the side of movement, as would be expected for covert motor preparation, but due instead to activation of positive polarity over the ipsilateral hemisphere. This finding requires closer consideration of the relation between the attention-directing EEG potentials and related imaging data.

Although previous work has proposed that attention-directing ADAN and LDAP are related to the frontoparietal attention network (Eimer et al. 2002; Hopf and Mangun 2000; Nobre et al. 2000b), it has not been acknowledged that there is a major paradox. In contrast to the attention-directing EEG potentials, which require subtraction of left and right directed attention conditions, frontoparietal network activation in imaging displays very little lateralization, being bilateral for attention to either visual field (Corbetta and Shulman 2002; Hopfinger et al. 2000). Macaluso et al. (2003) did find lateralization in some posterior areas, potentially explaining the LDAP, but none in anterior regions that might account for the ADAN. The present data go some way to resolve this paradox, because they reveal bilateral frontoparietal activation in EEG that at the same time shows a lateralization accounting for the ADAN. In addition, the parietal activation shifts rapidly in hemispheric balance, showing how asymmetries present in EEG might remain hidden in functional imaging due to its coarser temporal resolution. However, the data also introduce a new paradox.
Some imaging studies of spatial attention do show a modest asymmetry in frontoparietal activation, but they do so in terms of stronger activation contralateral to the direction of attention (Corbetta et al. 2002; Perry and Zeki 2000). In contrast, as explained above, the ADAN seems to be due to an ipsilaterally higher amplitude positive potential. One explanation for this paradox is that EEG and functional imaging may be preferentially sensitive to different aspects of the frontoparietal control of attention and intention, carried by transient and more sustained signals, respectively. Sustained attention-related activity from frontal and parietal cortex, as measured by single unit recordings (e.g., Colby et al. 1996; Di Pellegrino and Wise 1993), should also be present in EEG, but may be difficult to separate from other sources contributing to the CNV. Moreover, in our data, sustained activity may have been de-emphasized by the fixed cue-target delay, while it would have been stronger with a variable delay, forcing subjects to maintain spatial and response information on-line.

**Frontoparietal control of attention and intention**

As shown in Fig. 4, the ADAN corresponds in latency and covaries in amplitude with the P300 potential. The ADAN relation to the P300 may shed light on its role in the control of attention and intention. The P300 is associated with stimulus evaluation and is regarded as a manifestation of context updating (Donchin and Coles 1988). In line with this concept, the magnitude of the P300 increases with the information extracted from a stimulus and the extent to which the information can be used for response preparation (Gratton et al. 1990). At a neurophysiological level, the P300 is an inhibitory potential, evidenced in cortical disfacilitation (Deecke et al. 1984; Praamstra and Seiss 2005; Schupp et al. 1994; Tomberg and Desmedt 1998). The P300 comprises activity from different brain regions (Makeig et al. 2004) and the inhibition reflected in the P300 can have a task-specific distribution (Schupp et al. 1994). Together, these characteristics raise the interesting possibility that the frontoparietal EEG activation and the ADAN are a manifestation and focal lateralization of the P300, elicited by the updating of a task-defined preparatory state. In this study, the experimental context defined two alternative locations for spatial attention and two response sides. The arrow cue specified one location and/or response side as relevant, rendering alternative(s) irrelevant. We propose that the utilization of cue information for attentional orienting and response choice involves inhibition of the rejected behavioral options. That the frontoparietal network would be activated by the modification of an earlier established preparatory state finds support in the observation that termination of a preparatory state is likewise accompanied by frontoparietal activation (Shulman et al. 2002). Similarly relevant is evidence that parietal activation associated with attention shifts can be discrete in nature rather than sustained (Yantis et al. 2002).

Interpretation of the frontoparietal EEG activation as reflecting the modification of a preparatory state may be assimilated to the recognized role of the parietal cortex in redirecting attention and in change of movement plans (Andersen and Buneo 2002; Rushworth et al. 2001). Attentional and intentional aspects of this role are not necessarily lateralized to right and left hemisphere, at least for dorsal frontoparietal activations (Corbetta and Shulman 2002). Within the posterior parietal cortex, attention and intention-related activity may partly reflect regional specialization for eye movement and hand movement effector systems (Andersen and Buneo 2002; Rushworth et al. 2001), paralleled by a similar specialization in the prefrontal cortex (Simon et al. 2002; Wise et al. 1997). Under this perspective, the allocation of spatial attention, linked to eye-movements, and the preparation of a manual response engage different frontoparietal circuits, but these would not necessarily be distinguishable in EEG. On the other hand, there is also activity in the posterior parietal cortex, as well as the premotor cortex, that is effector-independent and common to different behaviors as attending, looking and pointing (Astafiev et al. 2003). This effector-independent activity can be explained by eye and hand effector systems using the same spatial information. In primate neurophysiology, effector-independent spatial activity in the posterior parietal cortex has been described as more widespread in localization than effector-specific activity (Calton et al. 2002), with a likely role in the representation of multiple potential responses, as has been found in the premotor cortex (Cisek and Kalaska 2002). The present data do not permit a definitive characterization of the frontoparietal EEG activation as effector-specific intentional or effector-independent spatial activity. Nonetheless, the finding that attention and motor preparation for one side did not elicit higher amplitude activation than motor preparation alone would seem to argue for effector-independent activity.

In summary, these data provide further evidence that previously described directing-attention potentials in human EEG are not only elicited by attention shifts, but also by the selection of hand movements. We have shown that these potentials, probably generated in the premotor cortex and the lateral occipital cortex, are associated with bilateral frontoparietal activation which is likewise indifferent to whether directional cues guide spatial attention or the side of a manual response. The frontoparietal activation captured in EEG is of a transient nature but shows nonetheless a distinct time course that specifies the temporal relations between frontal, parietal, and lateral occipital cortex activations following a directional cue. Crucially, the frontal EEG activation, and the frontoparietal activation as a whole, are not plausibly construed as movement preparatory EEG potentials. We propose instead that this activation is related to the modification of a preparatory state involving covert competition between the task-defined potential actions. The modification of such a preparatory state, i.e., the deselection or inhibition of a potential, task-defined response, might involve effector-specific neural activity or neural activity common to manual response selection and spatial attentional selection. Further research is necessary to distinguish between these alternatives and to map in more detail the relation between EEG and neuroimaging manifestations of the frontoparietal attention network.

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