

The instructed context of a motor task modulates covert response preparation and shifts of spatial attention

ELENA GHERRI,^a JOSÉ VAN VELZEN,^b AND MARTIN EIMER^a

^aSchool of Psychology, Birkbeck College, University of London, London, UK

^bGoldsmiths College, University of London, London, UK

Abstract

We investigated how covert response preparation is modulated by the instructed cognitive context of a motor task. Participants prepared left-hand or right-hand movements toward or away from the body midline, as indicated by a response cue (S1) presented prior to a go/no-go stimulus (S2). Different participants were instructed that response cues specified the response hand or movement direction, respectively. This emphasis on effector versus movement direction selection modulated lateralized ERP components triggered during the S1–S2 interval. Attention shifts during movement preparation were assessed by measuring ERPs to irrelevant visual probes. Enhanced N1 components were found for probes near the effector when effector selection was emphasized, but for probes near the movement target location when movement direction selection was emphasized. Results demonstrate strong top-down contextual biases on motor control and on the locus of spatial attention during response preparation.

Descriptors: Attention, Motor control, Response preparation, Cognitive control, Event-related potentials

During the preparation of a motor response, an abstract action goal is translated into the appropriate motor program that specifies the dimensions on which a movement varies (Keele, 1968, 1981; Rosenbaum, 1983). These movement dimensions are computed through a complex series of sensorimotor transformations where sensory spatial information about the current effector and target locations is eventually translated into an output pattern of motor commands and peripheral muscle activation. Studies of the neural mechanisms that are activated during response preparation have frequently used the “instructed delay period” paradigm, where a sensory cue specifies parameters of the movement to be prepared and is followed after a delay period by an imperative stimulus that signals whether to execute or withhold the prepared movement. Electrophysiological studies in macaques have found activity in several movement-related regions, such as motor and premotor cortices and posterior parietal cortex, during the instructed delay period (Alexander & Crutcher, 1990; Andersen, 1995; Kalaska & Crammond, 1995; Kurata, 1993; Prut & Fetz, 1999; Riehle & Requin, 1989; Wise, 1985). These premotor and parietal brain areas are characterized by highly specific neural connections (e.g., Matelli & Luppino, 2001), which form a series of largely segregated anatomic circuits (Luppino & Rizzolatti, 2000; Fadiga, Fogassi, Gallese, & Rizzolatti,

2000; Rizzolatti, Luppino, & Matelli, 1998), each dedicated to a specific sensorimotor transformation. For instance, a parieto-frontal circuit dedicated to the implementation of reaching movements connects the dorsal premotor cortex (PMd) to a specialized parietal area (parietal reach region, PRR) located within the medial intraparietal sulcus of macaque superior parietal lobe (Andersen & Buneo, 2002). Evidence from functional neuroimaging studies suggests a similar functional organization in humans (for a review, see Culham & Kanwisher, 2001). For example, the fronto-parietal activation found during the instructed delay interval of a reaching movement may be homologous to the activity of neural circuits that subservise reaching in monkeys (Filimon, Nelson, Hagler, & Sereno, 2007).

It is important to note that the sensorimotor transformations involved in the selection and activation of motor responses are not simply stimulus–response reflexes that are elicited in a rigid and invariant fashion whenever a specific type of movement is being prepared in response to a certain kind of stimulus (Jeannerod, 1997). To be flexible, the control of goal-directed behavior needs to take into account the contextual setting of motor tasks. Accordingly, sensorimotor processes involved in response selection and response preparation have been shown to be modulated in a top-down fashion by cognitive and motivational factors, such as the selection and evaluation of specific types of response-relevant sensory information, the presence of predictive relationships between different spatial and temporal parameters of a motor task, or the anticipated reward value of responses based on past experience. Recent neurophysiological studies have uncovered initial evidence for such top-down effects of cognitive content on motor control processes in prefrontal and

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Address reprint requests to: Elena Gherri, School of Psychology, Birkbeck College, University of London, Malet Street, London, WC1E 7HX, UK. E-mail: e.gherri@psychology.bbk.ac.uk

primary motor areas (for a review, see Johnson, Mason, & Ebner, 2001) as well as in parietal cortex (area LIP; for a review, see Gottlieb, 2007): When executed in different sensory, decisional, or motivational contexts, the selection of the same movement parameters can be accompanied by a quantitatively or qualitatively different activation pattern of anterior and posterior motor control regions.

In the present study, we used event-related brain potential (ERP) markers of cortical processes involved in the covert preparation of manual reaching movements to investigate whether and how such processes might be affected by a subtle manipulation of the contextual setting for a motor task. Because of their excellent temporal resolution, ERPs provide a useful tool to investigate covert response preparation processes. A number of recent studies have recorded ERPs during the instructed delay period of simple motor tasks that required the preparation of finger lift or key press responses (Eimer, Forster, Van Velzen, & Prabhu, 2005; Eimer & Van Velzen, 2006; Eimer, Van Velzen, Gherri, & Press, 2006; Mathews, Dean, & Sterr, 2006; Praamstra, Boutsen, & Humphreys, 2005; Van der Lubbe et al., 2000; Wauschkunn, Wascher, & Verleger, 1997). These studies have uncovered two lateralized ERP components that are elicited during covert response preparation and are likely to reflect preparatory activity in dorsal premotor and occipitotemporal areas involved in response programming. About 350 ms after the presentation of a response cue, ERPs were found to be more negative at anterior electrodes over the hemisphere contralateral to the cued response side relative to ipsilateral ERPs. Almost simultaneously, an ERP component of opposite polarity (an enhanced positivity contralateral to the cued response side) emerged at lateral posterior recording sites. Interestingly, these lateralized ERP components found during covert response preparation were remarkably similar to ERP components observed in other studies during cued shifts of spatial attention in tasks where the side of a forthcoming target was indicated by a central symbolic cue (cf. Eimer, Van Velzen, & Driver, 2002; Harter, Miller, Price, LaLonde, & Keyes, 1989; Hopf & Mangun, 2000; Nobre, Sebestyen, & Miniussi, 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994). In these tasks, the enhanced anterior negativity contralateral to the side of a cued attentional shift was termed Anterior Directing Attention Negativity (ADAN), and the posterior contralateral positivity was termed Late Directing Attention Positivity (LDAP). Because ERP components triggered during the instructed delay period of a motor task are very similar to the ADAN and LDAP observed during cued attention shifts, the same labels are now also being used to refer to the lateral anterior and posterior components that are elicited during covert response preparation.

The fact that similar lateralized ERP components are triggered during instructed shifts of spatial attention and during covert movement preparation provides support for the claim of the premotor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994) that shared sensorimotor control mechanisms are involved in attentional orienting and in the programming of motor responses. According to this theory, spatial attention is tightly coupled to functionally specialized brain circuits that direct action in space. The main difference between attention and action is that in the former case the pragmatic map is activated but the motor program for that specific action is not executed (Rizzolatti et al., 1994; Sheliga, Riggio, & Rizzolatti, 1994; Sheliga, Craighero, Riggio, & Rizzolatti, 1997). If the same sensorimotor circuits are responsible for directing both attention and action

toward the same location in space, attentional orienting and spatially directed response preparation should give rise to a very similar pattern of ERP activity, and this is exactly what has been observed in several recent studies (Eimer et al., 2006; Praamstra, 2006; Praamstra et al., 2005). Additional evidence for the assumption that covert response preparation and shifts of spatial attention are closely linked comes from previous studies where task-irrelevant visual probes were presented during the response preparation interval, either adjacent to the hand involved in an anticipated response or adjacent to the opposite uncued hand (Eimer & Van Velzen, 2006; Eimer et al., 2006). Here, enhanced visual N1 components were elicited to visual probes presented next to the cued response hand, relative to probes presented near the opposite uncued hand. Such N1 modulations strongly suggest that attention is shifted toward the location of the hand that is involved in an upcoming response, resulting in a spatially selective modulation of visual processing for probe stimuli that are presented near this hand.

Although there is now converging evidence that covert manual response preparation is associated with a systematic and replicable pattern of lateralized ERP components (ADAN, LDAP), it is not yet known whether these components are associated with the preparation of specific and dissociable spatial parameters of a prepared response. Response preparation usually involves the activation of an effector, the specification of a movement path, and the selection of the target location for a movement. Components such as the ADAN and LDAP that are triggered during response planning might be linked to one or more of these parameters. This issue could not be addressed in most previous ERP studies of response preparation where simple actions such as finger lift or button press responses were used, effector and movement target locations were spatially coincident, and movement direction was constant.

To begin to dissociate the effects of different movement parameters on ERP components elicited during response preparation, we have recently measured these components under conditions where response hand and movement direction were cued independently (Gherri, Van Velzen, & Eimer, 2007). Participants had to prepare and then execute one of four possible reaching movements with their right or left hand toward a target located on the right or left hemifield, and response precues provided either partial or full information about response hand or movement direction. The anterior ADAN component was found to be equally sensitive to effector and movement direction information. In contrast, the posterior LDAP component was substantially larger when response precues specified the effector for an upcoming movement than when they signaled movement direction instead, although this component was also reliably present when only movement direction information was provided. This suggests that the LDAP predominantly reflects mechanisms underlying effector selection, with only a limited contribution from processes involved in the specification of movement direction. The aim of the present study was to gain further insights into the processes involved in effector and movement direction selection during covert manual response preparation. Most importantly, we investigated for the first time with ERP measures whether and how these processes are modulated by top-down contextual factors. In different blocks, participants had to perform two different types of movement along the horizontal plane. In blocks with outward movements, they had to move one of their hands from a starting position located 5 cm to the left or right of the body midline toward an outer target location on the

same side (20 cm from the midline). During blocks with inward movements, start and target locations were reversed, that is, movements were now directed from an outer starting position toward the body midline (see Figure 1). At the start of each trial, a centrally presented visual cue (S1) signaled which of the two alternative movements had to be prepared. This response cue was followed after a 1000-ms interval by an imperative go/no-go stimulus (S2) that instructed participants to either execute or withhold the prepared movement. In addition, a task-irrelevant visual probe stimulus was presented on each trial. This probe appeared randomly and with equal probability at one of the four start or end positions for a movement on the left or right side, either during the covert response preparation interval (900 ms after cue onset), or during movement execution (200 ms after the onset of a manual response).¹

The critical manipulation of the present experiment was designed to investigate the role of top-down contextual factors during covert manual response preparation. Participants were randomly assigned to two groups that were given different instructions with respect to the nature of the response information provided by the cue. One group of participants was told that the response cue signaled whether the left or right hand had to be prepared for an upcoming response (effector cue instruction). The other group of participants was informed that the cue specified the direction (leftward or rightward) of an upcoming movement (direction cue instruction). Thus, even though cues always provided full response information for both groups of participants (i.e., they specified unequivocally which of the two alternative movements was to be prepared in a given trial), these two instructions either emphasized the selection of an effector or the selection of movement direction. If cortical processes involved in response selection can be biased in a top-down fashion by this subtle contextual manipulation, the pattern of ERP effects obtained during covert response preparation should differ systematically as a function of which instruction was provided.

Two sets of analyses were conducted. To obtain components sensitive to covert response preparation (ADAN, LDAP), ERPs triggered in the S1–S2 interval were measured for cues signaling a response on the left or right side, separately for inward and outward movements.² To investigate spatially specific modulations of visual processing during the covert response preparation interval that indicate shifts of spatial attention toward the cued response side, ERPs were also obtained in response to the visual

probe stimuli on the cued and uncued side, separately for probes presented at the start and end positions for manual movements.

ADAN and LDAP components were predicted to be differentially affected by movement type (inward vs. outward movements). The ADAN component was expected to be more pronounced during blocks where outward movements were being prepared, because for these movements, the spatial codes involved in effector and movement direction selection were always congruent (i.e., the left hand had to be moved toward the left or the right hand toward the right). In contrast, during blocks with inward movements, these two codes were incongruent (i.e., the left hand had to be moved toward the right or the right hand toward the left). If the ADAN component reflects processes involved in the selection of the left versus right hand as well as processes underlying the selection of a leftward versus rightward movement direction, as suggested by our previous study (Gherri et al., 2007), it should be strongly affected by the congruency versus incongruency of their respective spatial codes. In contrast to the ADAN, the posterior LDAP component primarily reflects effector selection (Gherri et al., 2007). Furthermore, results from an ERP study where ADAN and LDAP components were measured during cued shifts of tactile attention toward the left or right hand (Eimer, Forster, Fieger, & Harbich, 2004) have suggested that the selection processes that give rise to the LDAP are mediated by representations of *external* space. In this study, the LDAP (but not the ADAN) was larger in amplitude when hands were positioned far apart than when they were located closely together, in line with the assumption that external spatial coordinates play an important role for the LDAP component. If hand posture affected LDAP amplitudes in a similar fashion also during covert movement preparation, this component should be larger during the preparation of inward movements, where the external location of hands is more peripheral, than during outward movement preparation, where the hands are located close to the body midline (see Figure 1). The new question addressed in the present study was whether any such effects of movement type on ADAN and LDAP components would be modulated in a top-down fashion by the relative emphasis on effector selection or movement direction selection that differed between the two instruction groups.

If situational context of a motor task, as specified via response cue instructions, can affect response programming, such a top-down bias might also have an impact on shifts of spatial attention that are triggered as a result of manual response preparation processes. To investigate this possibility, we compared the effects of covert response preparation on visual ERPs to irrelevant probe stimuli for the two instruction groups. Based on earlier findings (Eimer & Van Velzen, 2006; Eimer et al., 2006), we expected to find enhanced N1 components for visual probes presented on the side cued for an upcoming movement relative to probes on the opposite uncued side. Such a result would further confirm the presence of spatially selective response preparation effects on visual processing, as postulated by the premotor theory of attention. The critical question was whether the locus of these attentional modulations of visual ERPs would shift from the initial starting position of a hand to the target position for an intended movement, or vice versa, depending on which instruction was provided. When effector selection is emphasized (effector cue instruction), effects of response preparation on visual processing, as reflected by enhanced N1 amplitudes, should be found for probes at the initial effector position, but not for movement target locations. In contrast, when movement

¹Visual probes were presented with equal probability during response preparation or during response execution in order to reduce their potential to be used as a temporal marker (i.e., as a warning signal that S2 presentation is imminent). However, ERPs were only measured for probes presented during the response preparation interval, but not for probes presented during response execution, as the latter are contaminated by motor, somatosensory, and visual components associated with response execution and vision of the moving hand.

²In addition to the two lateralized components on which our analyses were focused (ADAN and LDAP), another component that is typically elicited during the S1–S2 interval of cued response tasks is the contingent negative variation (CNV; Walter, Cooper, Aldridge, McCallum, & Winter, 1964). The CNV was not analyzed in our study because it is essentially nonlateralized (for a review, see Brunia & Van Boxtel, 2001), whereas our critical manipulations (movement types, response cue instructions) had an inherent left–right component and were designed to affect lateralized components such as ADAN and LDAP. CNV amplitudes are typically larger for more difficult tasks (e.g., Brunia, 1993), whereas task difficulty did not differ between different movement types or response cue instructions in our study (see Behavioral Performance).

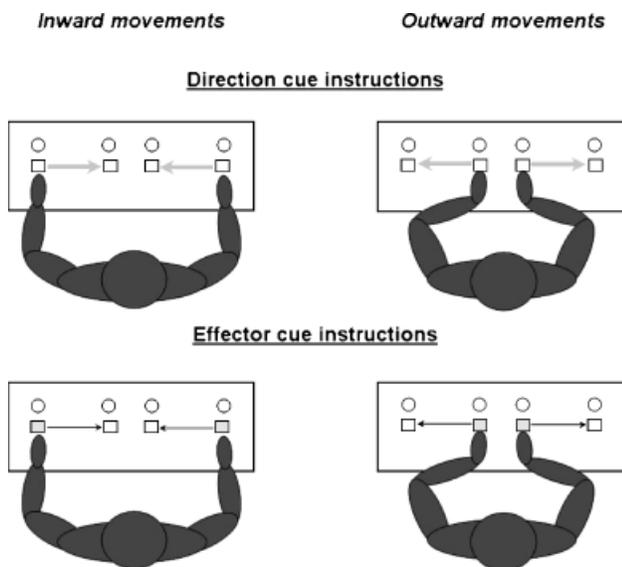


Figure 1. Schematic representation of the different movement types and instruction conditions. During inward movement (left side), start keys where hands were positioned during response preparation were located far apart, whereas target keys (i.e., end locations of movements) were positioned close to the body midline. During outward movements (right side), these positions were reversed, as start keys and hands were now located close to the body midline and movement targets were in the two outer positions. Top panels show the direction cue instruction condition where participants were informed that response cues specified the direction of a reaching movement toward the left or right side (represented by gray thick arrows). Bottom panels show the effector cue instruction condition where participants were told that response cues indicated whether the left or right hand had to be prepared for an upcoming movement (represented by start keys filled in gray). The location of the irrelevant visual probes that were presented either during response preparation or response execution is represented by the small circles above each start and target key.

direction is emphasized (direction cue instruction), the opposite pattern might emerge, with visual N1 enhancements now focused at the target location for a movement.

Methods

Participants

Twenty-five healthy volunteers participated in this experiment. Three were excluded due to poor eye gaze control in the cue–target interval (see below), and 2 others were excluded due to an insufficient number of trials after artifact rejection. Thus 20 participants remained in the sample. These were randomly assigned to two experimental groups of 10 participants that differed with respect to the response instructions given (see below). The group receiving effector cue instructions contained 3 men and 7 women (19–34 years old; average age: 25.3 years; 1 left-handed participant). The group receiving direction cue instructions contained 5 men and women (21–35 years old; average age: 28.6 years; all right-handed). All participants had normal or corrected-to-normal vision by self-report and were naïve as to the purpose of the experiment.

Apparatus, Stimuli, and Procedure

Participants sat in a dimly lit sound-attenuated cabin in front of a computer screen at a viewing distance of approximately 55 cm. A

custom-made response device was placed on the table just below the computer screen (see Figure 1). The device contained four response keys (two start keys and two target keys) that were horizontally aligned on a wooden panel (60 × 48 cm). This panel was tilted at an angle of 30°, and its midline was aligned with the screen center. Two infrared keys were used as start keys whereas the two target keys were normal response buttons. Infrared keys consisted of a transmitter and a 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 from the resting position, allowing the light beam of the transmitter LED to reach the receiver LED. Start and target keys were located in different positions in blocks that required inward or outward movements. During outward movements, start keys were located 5.5 cm to the left and right of the center of the panel, whereas the two target keys were placed further outward (25.5 cm from the center). During inward movements, these positions were swapped, with start keys located at the two outer positions and target keys at the two inner positions. Thus, the distance between each start and corresponding target key (movement length) was kept constant at 20 cm.

Each trial started with a 100-ms presentation of a visual response precue (S1) at fixation. This cue 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 fixation cross, located in the space between the two triangles, was present throughout the experimental blocks. The required movement for each trial was signaled by the direction of one of the triangles. For half of the participants, blue triangles were relevant, whereas for the other half, red triangles were relevant. Relevant left-pointing or right-pointing triangles were presented with equal probability to the left or right of fixation. On each trial, the response cue was followed after an empty interval of 1000 ms by the letter *G* or *S* (S2), indicating to execute (“go”) or withhold (“stop”) the movement. This letter was presented at fixation for 100 ms, replacing the fixation cross during this period. To investigate whether covert manual response preparation results in spatially selective modulation of visual processing, an irrelevant visual probe stimulus was presented on each trial, either 900 ms after cue onset (i.e., 200 ms prior to the onset of the imperative go/no-go stimulus) or 200 ms after movement onset, as recorded by the infrared keys. Probes consisted of 100 ms of illumination of one of four ensembles of green LEDs that were positioned 2.5 cm above each start and target key on the left and right side (see Figure 1). Participants were instructed to completely ignore these probe stimuli throughout.

The experiment consisted of 16 experimental blocks of 96 trials each. A go S2 was presented on 80 trials per block, and a no-go S2 on the remaining 16 trials. On each trial an irrelevant visual probe was presented with equal probability and in random order next to one of the four start or target keys, either 900 ms before cue onset or 200 ms after movement onset. Thus every block contained five go trials and one no-go trials for each combination of cued response side (left vs. right), probe location (next to hands/start keys vs. next to movement target keys), probe side (left vs. right), and probe onset (early vs. late). Trials were presented in a pseudorandom sequence. In eight successive blocks, participants performed one of two different types of movements. In “inward movement” blocks, they had to prepare a movement from an outer start key toward an inner target key (i.e., toward the body midline). In “outward movement” blocks,

they had to prepare a movement from an inner start key toward an outer target key (i.e., away from the body midline). The order in which these two blocked movement type conditions were delivered was counterbalanced across participants. One training block of 48 trials was run before each movement type condition.

Participants were randomly assigned to two different instruction groups. Ten participants were told that the response cue specified which effector (right vs. left hand) to prepare in anticipation of an upcoming go S2 (“effector cue instruction”). The other 10 participants were told instead that the response cue indicated the direction of the movement (leftward vs. rightward) to be prepared (“direction cue instruction”). These task instructions were shown on the computer screen prior to the start of each block. All participants placed their forearms on the response panel with their index fingers on the start keys (resting position) and maintained a body posture such that their midline was aligned with the center of the screen and response panel. They were explicitly encouraged to maintain central eye fixation and to use the information provided by S1 to covertly prepare the cued movement while maintaining the resting position with their hands on the start keys until the imperative stimulus (S2) was displayed on the screen.

On go trials, participants had to perform a movement from one start to one target key on the side that was indicated by the response cue, press the target key, and then place their hand back on the infrared start key in the resting position in order to start the next trial. Therefore, the time interval between the onset of the imperative stimulus on one trial and the onset of the response cue on the next trial was a variable function of total movement time. The next response cue was presented 600 ms after the hand had returned to the start key. On no-go trials, participants had to leave their hands on the start keys and to wait for the next response cue presentation. Here, the interval between the onset of the imperative stimulus on one trial and the onset of the response cue on the next trial was randomly selected between 1850 ms and 2050 ms.

Electroencephalogram (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 electro-oculogram (EOG) was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 k Ω , and the impedances of the earlobe electrodes were kept as equal as possible. Data were recorded with a band-pass filter from 0 to 40 Hz and a digitization rate of 200 Hz. Trials with eyeblinks (Fpz exceeding $\pm 80 \mu\text{V}$), horizontal eye movements (HEOG exceeding $\pm 30 \mu\text{V}$), or other artifacts (a voltage exceeding $\pm 80 \mu\text{V}$ at any electrodes) in the S1–S2 interval were excluded prior to data analysis. To detect systematic deviations of eye position indicating residual tendencies to move the eyes toward the side of the cued response, averaged HEOG waveforms in the S1–S2 interval in response to left versus right cues were examined for each participant. HEOG deviations exceeding $\pm 3 \mu\text{V}$ led to the disqualification of 3 participants. For the 20 participants kept in the sample, overall residual HEOG deviation (calculated as a difference between grand averaged ERP elicited by left vs. right cues) was below 0.45 μV throughout the S1–S2 interval. ERPs were averaged relative to a 100-ms pre-S1 baseline for the 1000-ms time interval following S1 onset.

One set of analyses focused on ADAN and LDAP components elicited during the covert response preparation interval. ERP mean amplitude values were obtained for a time window between 400 and 700 ms after S1 onset (where the ADAN and the early phase of the LDAP was observed in earlier response precueing experiments), and for a 700–900-ms postcue time window (where the later phase of the LDAP was previously observed). An initial analysis assessed the overall presence and distribution of ADAN and LDAP components on the basis of ERP mean amplitudes to response cues instructing participants to prepare a response on the left versus right side, collapsed across both movement types (inward vs. outward) and instruction (effector vs. direction cue), with a three-way repeated measures analysis of variance (ANOVA) conducted separately for lateral anterior, central, and posterior sites. In these analyses the factors cued response side (left vs. right), laterality (electrode ipsilateral vs. contralateral to cued response side), and 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) were used as within-subjects variables. The presence of ADAN and LDAP components are reflected by significant main effects of the factor laterality. Next, we analyzed the effects of movement type (inward vs. outward) and, critically, possible top-down effects of response instruction on these lateralized components. These analyses were restricted to the electrode pairs where ADAN or LDAP components were elicited most reliably. ERP mean amplitude values obtained for the 400- and 700-ms and for the 700–900-ms postcue time windows were entered into a four-way mixed design ANOVA with the factor instruction (effector vs. direction cue instruction) as the between-subject variable and cued response side (left vs. right), laterality (electrode ipsilateral vs. contralateral to cued response side), and movement type (inward vs. outward) as within-subject variables.

The second set of analyses was conducted for visual ERPs in response to probe stimuli presented 900 ms after S1 onset. These were computed for the 300-ms interval after probe onset (relative to a 100-ms baseline prior to probe onset), separately for each combination of probe location (next to hands/start keys vs. next to target keys) and movement preparation (probe located in hemisphere of cued movement vs. opposite hemisphere), but were collapsed across both movement types (inward and outward).³ Because inspection of these visual ERPs suggested that they might be affected by overlapping slow wave activity, a high-pass filter (2 Hz, 48 dB/oct) was applied to the raw EEG data (prior to EEG epoching, baseline correction, artifact rejection, and averaging) to remove this activity. All analyses of visual ERPs reported here are based on these filtered data. Mean amplitudes were computed within a latency window centered on the peak amplitude of P1 and N1 components (P1: 90–120 ms poststimulus; N1: 140–180 ms poststimulus), and were analyzed with a five-way mixed design ANOVA, separately for midline electrodes (Fz, Cz, Pz) and for lateral anterior, central, and posterior sites. Analyses included the factor instruction (effector vs. direction cue instruction) as a between-subjects variable and the fac-

³Note that as a result of collapsing across inward and outward movements, these visual ERPs show the combined response to probe stimuli at near and far locations. For example, for blocks where inward movements were required, probes next to the start key/effector were located at the two outer locations, whereas these probes were located at the two inner locations in blocks with outward movements (see Figure 1).

tors probe location (next to hands/start keys vs. next to target keys), cued response side (probe located on the side of the cued movement vs. on the opposite side), hemisphere (left vs. right, for lateral electrodes only), and electrode site (F7/8, F3/4, FC5/6 for anterior electrodes; C3/4, T7/8, CP5/6 for central electrodes; OL/R, P3/4, P7/8 for posterior electrodes; Fz, Cz, Pz for midline electrodes) as within-subjects variables.

Behavioral performance was assessed to confirm that there were no systematic differences in task difficulty between inward and outward movements and between effector and direction cue instructions. Both reaction times (RTs, i.e., latencies of start key responses) and movement times (MTs, i.e., intervals between start key and target key responses) were measured. All trials with missing and premature responses (i.e., start key responses prior to S2 onset), with RTs shorter than 100 ms (anticipations) or longer than 1000 ms, and with MTs exceeding 1000 ms were excluded from analysis. RTs and MTs recorded in the remaining correct go trials were separately entered into a three-way mixed design ANOVA with instruction (effector vs. direction cue) as the between-subjects variable and movement type (inward vs. outward) and response hand (left vs. right) as within-subjects variables. In these analyses, main effects of the factors movement type or instruction would indicate that there were task difficulty differences between conditions.

All statistical analyses were conducted with a sample of 20 participants. Follow-up analyses conducted separately for each instruction group were carried out over a sample of 10 participants each. For all analyses, Greenhouse–Geisser adjustments to the degrees of freedom were applied where appropriate.

Results

Behavioral Performance

RTs did not differ between inward and outward movements ($M = 379$ ms, $SD = 60$ ms and $M = 371$ ms, $SD = 53$ ms, respectively), $F(1,18) = 0.6$, $MSE = 1848$, $p = .4$, or between groups with effector ($M = 370$ ms, $SD = 58$ ms) and direction cue instructions ($M = 380$ ms, $SD = 50$ ms), $F(1,18) = 0.17$, $MSE = 11,703$, $p = .7$. A main effect of response hand, $F(1,18) = 15.0$, $MSE = 194$, $p < .001$ was due to the fact that RTs were faster for left-hand than for right-hand movements ($M = 370$ ms, $SD = 50$ ms vs. $M = 380$ ms, $SD = 56$ ms). MTs did not differ between effector and direction cue instruction groups ($M = 266$ ms, $SD = 57$ and $M = 275$ ms, $SD = 146$ ms, respectively), $F(1,18) = 0.03$, $MSE = 49,156$, $p = .9$, but were faster for outward relative to inward movements ($M = 257$ ms, $SD = 102$ ms vs. $M = 283$ ms, $SD = 119$ ms), $F(1,18) = 7.9$, $MSE = 1,732$, $p < .011$. This difference was only present with effector cue instructions ($M = 242$ ms, $SD = 52$ ms vs. $M = 290$ ms, $SD = 67$ ms) but not with direction cue instructions ($M = 277$ ms, $SD = 159$ ms vs. $M = 273$ ms, $SD = 136$ ms), as reflected by a Movement Type \times Instruction interaction, $F(1,18) = 5.5$, $MSE = 466$, $p < .030$. In contrast to RTs, MTs were shorter for right-hand as compared to left-hand movements ($M = 262$ ms, $SD = 106$ ms vs. $M = 279$ ms, $SD = 111$ ms); main effect of response hand: $F(1,18) = 12$, $MSE = 466$, $p < .003$. Premature responses (before S2 onset) occurred on 1% of all trials. Anticipations were measured in 0.1% of all go trials, RTs beyond 1000 ms in 0.5% of all go trials, and MTs beyond 1000 ms in 0.16% of all go trials. On 17.7% of all no-go trials, an index finger movement was registered by one of the infrared response

keys. On 16.4% of all go trials, response onset latencies were longer than 1000 ms or no manual responses were recorded.⁴

Laterized ERPs Components Triggered during Reaching Movement Preparation

Figure 2 shows ERPs in the 900-ms interval after response cue onset at lateral anterior, central, and posterior electrodes ipsilateral (dashed line) and contralateral (solid line) to the side of cued movement. Waveforms are collapsed across different movement types (inward vs. outward) and instruction groups (effector vs. direction cue instructions). As expected, both ADAN and LDAP components were elicited during the covert movement preparation interval (see Figure 2, right panels, for scalp distribution). The presence of the ADAN was confirmed by a main effect of laterality at anterior electrode pairs during the 400–700-ms postcue interval, $F(1,18) = 8.1$, $MSE = 0.16$, $p < .011$. There was also a Laterality \times Electrode Site interaction, $F(2,36) = 15.7$, $MSE = 0.08$, $p < .001$, and follow-up analyses conducted separately for each anterior electrode pair confirmed the presence of a reliable ADAN at F3/4, $F(1,18) = 30.5$, $MSE = 0.07$, $p < .001$, and at F7/8, $F(1,18) = 5.1$, $MSE = 0.08$, $p < .036$, but not at FC5/6, $F(1,18) = 0.18$, $MSE = 0.09$, $p = .68$.

As can be seen in Figure 2, the LDAP component was present at central and posterior electrode pairs. In the 400–700-ms postcue interval, main effects of laterality, both $F(1,18) > 15.7$, $MSE < 1.1$, both $p < .001$, were obtained at lateral central and posterior electrodes, reflecting the early phase of the LDAP. These were accompanied by Laterality \times Electrode Site interactions, both $F(2,36) > 9.7$, both $p < .002$, and follow-up analyses revealed the presence of a significant early LDAP at all posterior electrode site, all $F(1,18) > 27.7$, $MSE < .59$, all $p < .001$, as well as at T7/8 and CP5/6, both $F(1,18) > 9.7$, $MSE < .24$, both $p < .006$, approaching significance at C3/4, $F(1,18) = 3.8$, $MSE = 0.21$, $p = .067$. During the later analysis window (700–900 ms poststimulus), a significant laterality effect was present at posterior electrode sites, $F(1,18) = 25.7$, $MSE = 1.03$, $p < .001$, reflecting the later phase of the LDAP. This effect only approached significance at central electrode sites, $F(1,18) = 3.9$, $MSE = 0.7$, $p = .065$.

To investigate the effects of movement type (inward vs. outward) and instruction (effector vs. direction cue) on ADAN and LDAP components, additional analyses were carried out for the two electrode pairs where these components were most reliably elicited (F3-F4 for the ADAN, P7-P8 for the LDAP; see Figure 2). Figure 3 shows ERPs elicited at these electrodes during inward and outward movement preparation (panels A–D), together with difference waveforms obtained by subtracting ERPs at electrodes contralateral to the side of cued movement from ipsilateral electrodes (panels E and F). In these difference waveforms, a contralateral negativity is indicated by positive values (downward-going deflections) and a contralateral positivity by negative values (upward-going deflections).

As can be seen in Figure 3 (top panels), the ADAN component was clearly present at F3-F4, main effect of laterality in the 400–700-ms postcue interval: $F(1,18) = 30.5$, $MSE = 0.07$, $p < .001$, but was more pronounced during outward as compared to inward movement preparation. This was substantiated by a significant Laterality \times Movement Type interaction,

⁴The relatively high percentage of false alarms and missed responses is in part due to the fact that the infrared system used to measure manual response onset did not always operate with absolute reliability.

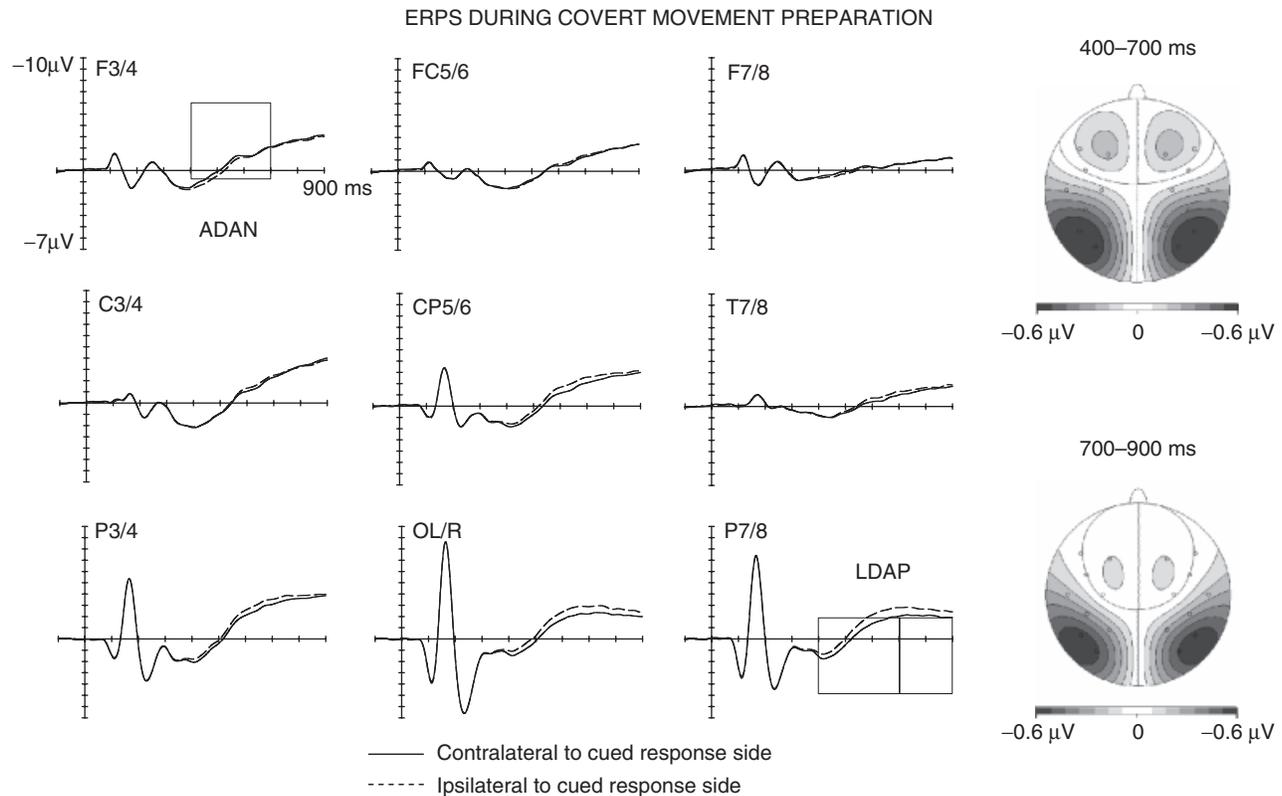


Figure 2. Grand-averaged ERPs elicited in the 900-ms interval following response cue onset at lateral anterior, central, and posterior electrode pairs ipsilateral (dashed line) and contralateral (solid line) to the side of the cued response. ERPs are collapsed across trials with inward and outward movements and both response instruction groups. The measurement windows used to compute ADAN amplitudes (400–700 ms after cue onset) and LDAP amplitudes (400–700 and 700–900 ms postcue) are marked with boxes. Right panels show scalp distributions of ADAN and LDAP components in the 400–700-ms and 700–900-ms intervals. Maps represent differences between brain activity observed over hemisphere ipsi- and contralateral to the cued response side. They were constructed by spherical splines interpolation (see Perrin, Pernier, Bertrand, & Echallier, 1989) after mirroring the difference waveforms to obtain symmetrical but inverse amplitude values for both hemispheres. Amplitudes range between 0.6 and 0.6 μV ; contour lines represent changes of 0.1 μV .

$F(1,18) = 6.7$, $MSE = 0.04$, $p < .02$. However, follow-up analyses conducted separately for each movement type revealed that the ADAN was significantly present not only during outward movement preparation, $F(1,18) = 29.9$, $MSE = 0.065$, $p < .001$, but also when inward movements were being prepared, $F(1,18) = 9.7$, $MSE = 0.04$, $p < .006$. In contrast, the difference between effector and direction cue instructions had no effect on the ADAN, $F(1,18) = 2.4$, $MSE = 0.07$, $p = .14$, and there were also no $\text{Laterality} \times \text{Movement Type} \times \text{Instruction}$ interactions, $F(1,18) = 0.16$, $MSE = 0.04$, $p = .7$.⁵

Figure 3 (bottom panel) shows the LDAP component at lateral posterior electrode pair P7-P8. During the 400–700-ms measurement interval, a main effect of laterality, $F(1,18) = 28.9$, $MSE = 0.6$, $p < .001$, confirmed the presence of the early phase of the LDAP, which was not modulated by the difference between inward and outward movements, $\text{Laterality} \times \text{Movement Type}$: $F(1,18) = 0.15$, $MSE = 0.11$, $p = .7$. In the subsequent 700–900-

ms time window, the late phase of the LDAP was reliably present, main effect of laterality: $F(1,18) = 23.4$, $MSE = 0.59$, $p < .001$. As can be seen in Figure 3 (panel F), this late LDAP was more pronounced during inward as compared to outward movement preparation, as reflected by a significant $\text{Laterality} \times \text{Movement Type}$ interaction, $F(1,18) = 5.2$, $MSE = 0.22$, $p < .035$. Follow-up analyses conducted separately for each movement type revealed that the late phase of the LDAP was significantly present not only during inward movement preparation, $F(1,18) = 19.8$, $MSE = 0.59$, $p < .001$, but also when outward movements were being prepared, $F(1,18) = 15.6$, $MSE = 0.24$, $p < .001$.

Importantly, and in contrast to the ADAN, the LDAP was systematically affected by the type of instruction that participants received with respect to the response cue. This differential instruction effect is illustrated in Figure 4, which shows ERPs elicited at P7-P8 during the preparation of inward and outward movements and the resulting difference waveforms, separately for the group of participants that had received direction cue instructions (top panels) and for the effector cue instruction group (bottom panels). When participants were told that the response cue specified movement direction (see Figure 4, top panels), the early phase of the LDAP component was more pronounced during outward movement preparation (i.e., movements directed

⁵Follow-up analyses conducted separately for the two different movement types confirmed the absence of significant $\text{Laterality} \times \text{Instruction}$ interactions during inward movements, $F(1,18) = 2.7$, $MSE = 0.04$, $p = .12$, as well as during outward movements, $F(1,18) = 0.84$, $MSE = 0.065$, $p = .37$.

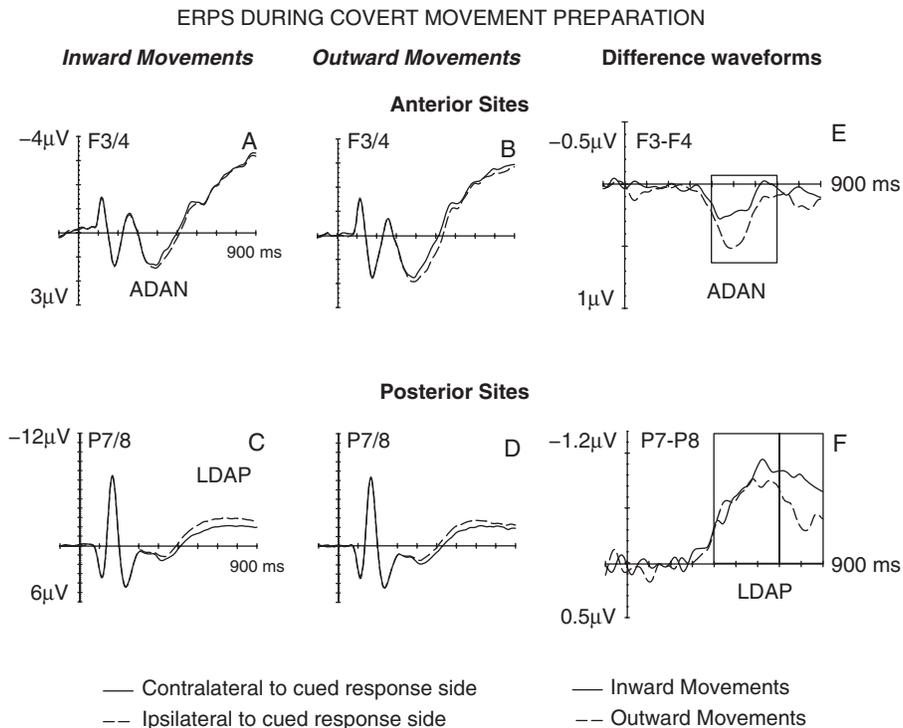


Figure 3. Grand-averaged ERPs elicited in the 900-ms interval after response cue onset at anterior F3/4 (top panels) and posterior P7/8 (bottom panels) electrode pairs. Panels A, B, C, and D show ERPs ipsilateral (dashed line) and contralateral (solid line) to the side of the cued response, separately represented for inward and outward movement preparation. Panels E and F (right side) show difference waveforms generated by subtracting ERPs elicited contralateral from ERPs elicited ipsilateral to the side of the cued response, separately for inward (solid line) and outward movement preparation (dashed line). Enhanced negativities contralateral to the side of the cued response are reflected by positive values (downward deflections) and enhanced contralateral positivities are reflected by negative values (upward deflections). Box markers indicate the ADAN and LDAP measurement windows.

away from the body midline) than during inward movement preparation (i.e., movements toward the body midline). In contrast, with effector cue instructions (see Figure 4, bottom panels), the early LDAP was larger during inward movement preparation (when hands were located further apart) than during outward movement preparation (when hands were located close to the midline). This is further illustrated in panels F and H of Figure 4, which show the absolute size of the LDAP amplitudes for the 400–700-ms and the 700–900-ms time intervals, obtained by subtracting mean ERP amplitudes at electrode ipsilateral to the cued response side from mean amplitudes obtained at the corresponding contralateral electrode, separately for inward (black bars) and outward movements (gray bars). This pattern of results was substantiated by a significant *Laterality × Instruction × Movement Type* interaction, $F(1,18) = 9.5$, $MSE = 0.114$, $p < .006$, in the 400–700-ms postcue time window. Follow-up analyses were conducted separately for the two different instruction groups. For participants receiving direction cue instructions, a reliable *Movement × Laterality* interaction, $F(1,9) = 7.4$, $MSE = 0.056$, $p < .024$, confirmed that the early LDAP was larger during outward movement preparation. For participants with effector cue instructions, this interaction was almost significant, $F(1,9) = 4.0$, $MSE = 0.17$, $p = .07$, due to the strong trend for a larger early LDAP during the preparation of inward movements. During the late phase of the LDAP (700–900-ms postcue), no *Laterality × Instruction* or *laterality × Instruction × Movement Type* interactions were present, $F(1,18) = 0.02$,

$MSE = 0.62$, $p = .9$ and $F(1,18) = 0.62$, $MSE = 0.22$, $p = .44$, respectively.

Visual ERPs to Task Irrelevant Probe Stimuli

Figure 5 shows visual ERPs elicited by irrelevant visual probe stimuli presented 900 ms after response cue onset, displayed separately for participants with direction cue instructions (top) and effector cue instructions (bottom) and for trials where probes were presented next to the hands/start keys (left) or next to the target keys (right). Solid lines represent ERPs to probes presented on the side of a cued movement, and dashed lines represent ERPs to probes on the opposite uncued side. As can be seen from Figure 5, advance information about the side of a to-be-prepared response had a systematic effect on the processing of visual probes, as N1 components tended to be generally larger for probes that were presented on the cued response side. However, and importantly, the spatial locus of this response preparation effect on visual N1 amplitudes was strongly modulated by response cue instructions. For participants who were told that the response cue specified the direction of an upcoming movement (direction cue instruction), a modulatory effect of response preparation on visual N1 components was present for probes presented next to the cued versus uncued movement target location, whereas no such effect emerged for probes that were presented next to the hands/start keys (Figure 5, top panel). In contrast, participants who were informed that the cue specified the hand to be prepared (effector cue instruction) showed larger effects of

ERPS DURING COVERT MOVEMENT PREPARATION

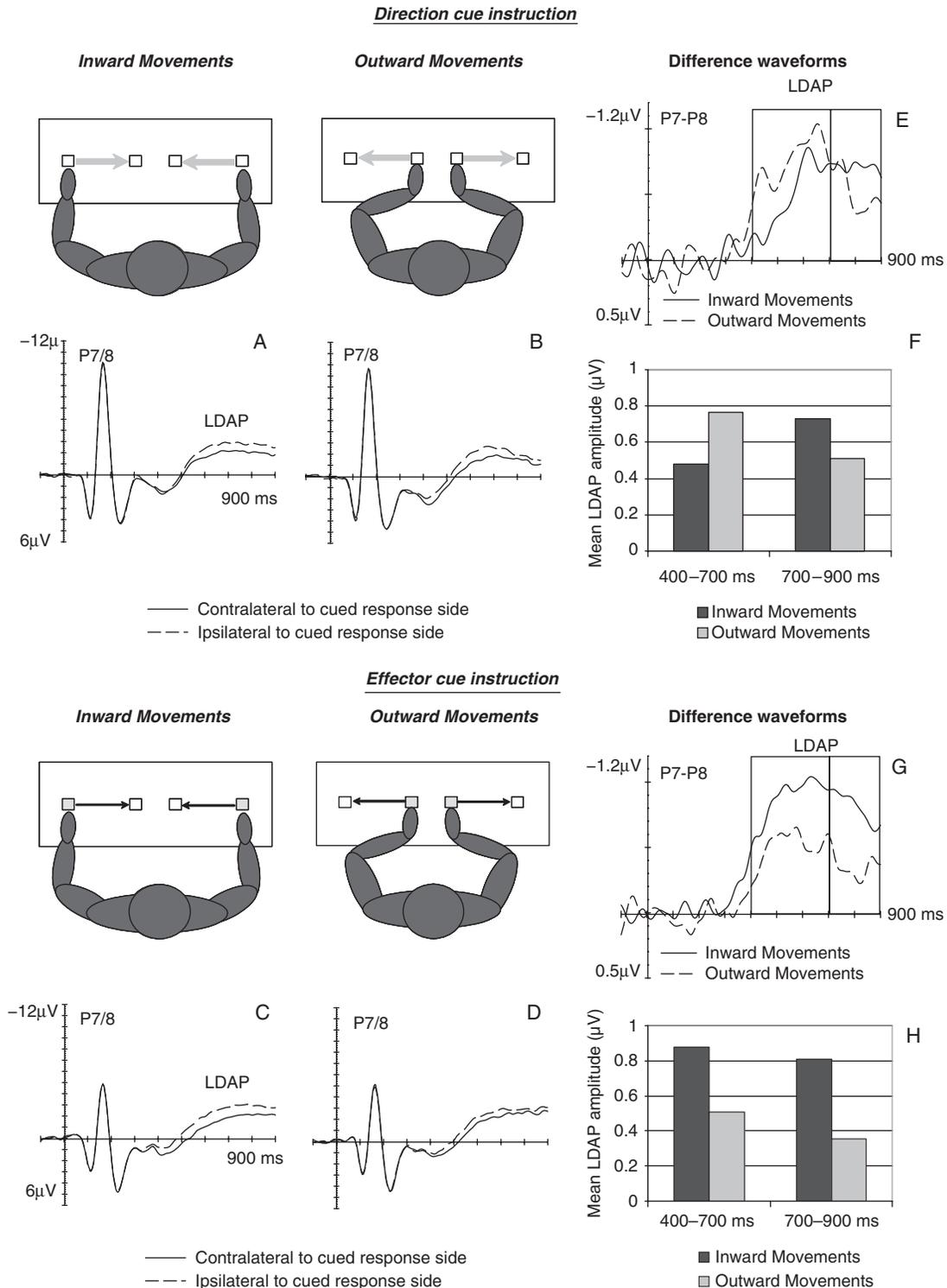


Figure 4. Grand-averaged ERPs elicited in the 900-ms interval after response cue onset at posterior electrode pair P7/8, shown separately for the participants with direction cue instructions (top panels) and for participants with effector cue instructions (bottom panels). Panels A–D show ERPs ipsilateral (dashed line) and contralateral (solid line) to the side of the cued response, separately for inward and outward movement preparation. Panels E and G (right side) show difference waveforms generated by subtracting ERPs elicited contralateral from ERPs elicited ipsilateral to the side of the cued response, separately for inward (solid line) and outward movement preparation (dashed line). Box markers indicate the LDAP measurement windows. Panels F and H (right side) show LDAP amplitudes obtained at P7/8 by subtracting ERP mean amplitudes at electrode ipsilateral to the cued response side from mean amplitudes obtained at the corresponding contralateral electrode in the 400–700-ms and 700–900-ms time intervals, separately for inward movement (black bars) and outward movements (gray bars).

ERPS TRIGGERED BY VISUAL PROBE STIMULI

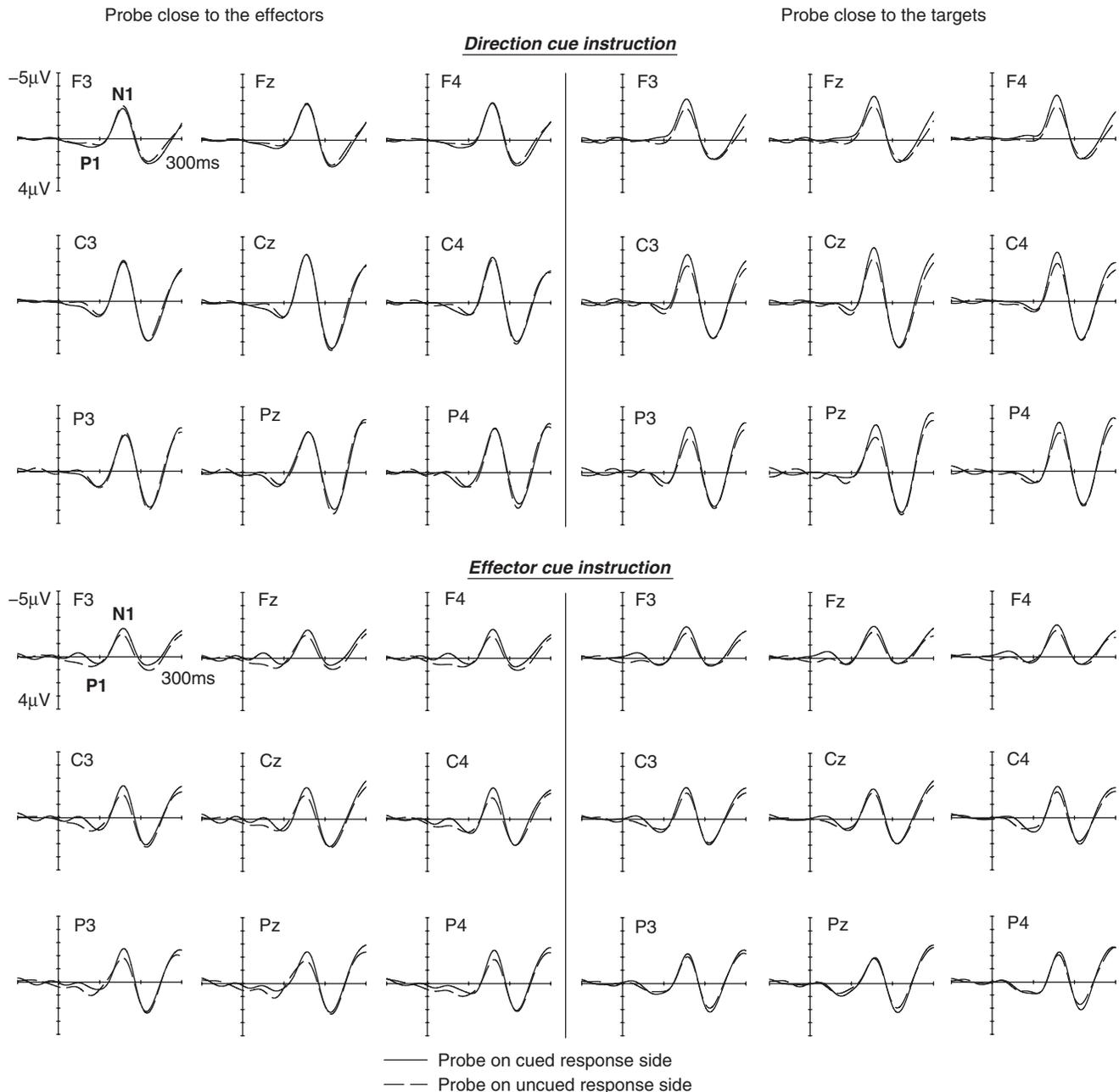


Figure 5. Grand-averaged visual ERPs elicited by visual probe stimuli delivered 900 ms after response cue onset, obtained on the basis of high-pass filtered raw EEG data and shown separately for probes located next to the initial position of the hands on the start keys (left panels) and for probes located next to the target keys (right panels). Solid lines show ERPs triggered by visual probes presented on the side of a cued response, and dashed lines show ERPs elicited on the opposite uncued side. Visual ERPs are shown separately for the group of participants that received direction cue instructions (top panels) and for the group that received effector cue instructions (bottom panels).

response preparation on visual N1 components when probes were presented close to the hands than when they were located next to the response target keys (Figure 5, bottom panel).

These informal observations were substantiated by statistical analyses. Although there were no significant response cueing effects on visual P1 amplitude (90–120 ms poststimulus), the N1 component to visual probes was strongly modulated by movement preparation. In the N1 time range (140–180 ms poststim-

ulus), main effects of cued response side on ERP mean amplitudes were present at lateral posterior, lateral central, lateral frontal, and midline sites, all $F(1,18) > 5$, all $MSE < 1.95$, all $p < .04$, demonstrating that N1 amplitudes were generally enhanced for visual probes that were presented on the side of a cued manual reaching movement. However, this effect was jointly modulated by response cue instructions (emphasizing effector or movement direction) and the location of the visual probes (next

to the hands or next to the target keys), as reflected by Cued Response Side \times Probe Location \times Instruction interactions that were significant at all lateral posterior, lateral central, and midline sites, all $F(1,18) > 6.6$, all $MSE < 0.7$, all $p < .019$, whereas this interaction approached significance at lateral frontal electrodes, $F(1,18) = 4.2$, $MSE = 0.7$, all $p = .055$.

This three-way interaction was further investigated in follow-up analyses carried out separately for each of the four combinations of response cue instruction (effector vs. direction cue) and probe location (next to the hands vs. next to the target keys). For participants who were informed that the cue specified the direction of an upcoming response, a significant N1 modulation for probes presented close to the cued versus uncued target key emerged at all electrode sites, all $F(1,9) > 9.6$, all $MSE < 1.1$, all $p > .013$, whereas no such modulation emerged when probes were presented close to the cued versus uncued hand, all $F(1,9) < 1$, $MSE < 2$, all $p > .65$. For participants who were told that the response cue indicated the hand to be prepared for an upcoming movement, significant N1 modulations were found for probes presented close to the cued versus uncued hand at lateral frontal, lateral central, lateral posterior, and midline electrode sites, all $F(1,9) > 5.7$, $MSE < 0.8$, all $p < .041$. In contrast, no reliable effects of cued response side emerged for probes that were presented close to the cued versus uncued target key, all $F(1,9) < 3.3$, $MSE < 1.5$, all $p > .103$.

Discussion

To investigate cortical processes activated during the programming of manual reaching movements and to find out whether and how such processes might be susceptible to a top-down bias by contextual factors, we measured ERP markers of covert manual response preparation (ADAN and LDAP components) and spatially selective visual processing (visual N1 component) in an instructed delay period paradigm, where participants prepared manual reaching movements as instructed by response cues presented at the start of each trial. Analyses of behavioral data confirmed that there were no systematic differences in task difficulty between different movement types or response cue instructions, thus making it unlikely that ERP components elicited during the S1–S2 interval would be affected by factors such as anticipated cognitive effort or task complexity.

Several results obtained in this study confirmed findings from other recent ERP investigations of covert manual response preparation (e.g., Eimer & Van Velzen, 2006; Eimer et al., 2005, 2006; Gherri et al., 2007; Mathews et al., 2006; Praamstra, 2006; Praamstra et al., 2005; Van der Lubbe et al., 2000; Wauschkuhn et al., 1997). As expected, ADAN and LDAP components were triggered in the interval between the response cue and the subsequent imperative go/no-go stimulus (see Figure 2), thus confirming that these components can be reliably observed during covert response preparation. The anterior ADAN component was larger in blocks where outward movements had to be prepared than in blocks where inward movements were required (Figure 3, top panel). With outward movements, the spatial codes involved in effector and movement direction selection were always compatible (e.g., when preparing a leftward movement with the left hand), whereas these codes were always incompatible for inward movements (e.g., when preparing a rightward movement with the left hand). The observation that the ADAN component was attenuated when spatial codes were incompatible

provides further evidence that the ADAN reflects the joint contribution of processes involved in the selection of the left versus right hand and of processes that underlie the selection of a leftward versus rightward direction for a movement (see also Gherri et al., 2007).

In contrast to the ADAN, the late phase of the LDAP component was more pronounced for inward as compared to outward movements (Figure 3, bottom panel). This difference is most likely due to the fact that initial hand positions were different for these two types of movements. During the preparation of inward movements, hands were placed much further apart than during the preparation of outward movements, where they were positioned close together (see Figure 1). The distance of effectors from the body midline has previously been found to modulate the LDAP during covert shifts of tactile attention to the left or right hand (Eimer et al., 2004). The current results demonstrate that effector position affects LDAP amplitudes not just during spatial orienting but also during covert response preparation, and thus suggest that the LDAP primarily reflects the selection of response hands rather than movement direction (as already suggested by our previous findings; see Gherri et al., 2007). Furthermore, they also imply that this selection is mediated by representations that code the location of the hands in terms of external space (i.e., their distance from the body midline). This conclusion is further supported by the results of a recent unpublished study from our laboratory. This study was similar to the experiment reported here, except that start and end positions for all reaching movements were now equidistant from the body midline, so that movement paths were always parallel to the median plane. In different blocks, these movements were either executed near to the body midline (5 cm to the left or right) or at a distance of 25 cm on the left or right side. Although the ADAN was unaffected by this distance manipulation, the LDAP was significantly larger during the preparation of far as compared to near movements, again suggesting that this component is sensitive to the representation of effector locations in an external spatial coordinate system.

The critical new question addressed in the present study was whether cortical covert response preparation processes are modulated by top-down contextual effects. For different groups of participants, instructions either stressed the link between response cues and effector selection (effector cue instruction) or the link between response cues and the direction of an upcoming movement (direction cue instruction). Even though all response cues were, in fact, informationally equivalent regardless of which instruction was provided (i.e., they always specified which of two alternative reaching movements would have to be executed in response to an upcoming go stimulus), this instruction manipulation still had systematic effects on the posterior LDAP component as well as on visual N1 components triggered in response to task-irrelevant probe stimuli. The differential effect of instructions on the LDAP is shown in Figure 4. When instructions emphasized effector selection, the initial phase of the LDAP component in the 400–700-ms time window after response cue onset was larger for inward than for outward movements (Figure 4, bottom panel), that is, for the movement type where hands were wide apart during response preparation. This result is in line with the general assumption that the LDAP primarily reflects the selection of effector locations that are mediated by representations of external space (see above). However, and critically, when instructions emphasized movement direction selection instead, this pattern was reversed, as the early phase of the LDAP was

now more pronounced during the preparation of outward movements. When coded in terms of movement direction, outward movements are associated with a stronger spatial left/right bias than inward movements, as outward movements were directed toward the left or right periphery, whereas inward movements were directed toward the body midline (Figure 4, top panel). Overall, the results as shown in Figure 4 provide clear evidence for a top-down contextual bias on cortical response selection processes: Depending on which instruction was provided, priority was given either to the selection of an effector or to the selection of a specific response direction. LDAP amplitudes were enhanced whenever the prioritized response parameter was associated with a more lateral spatial location and attenuated whenever this parameter specified a location closer to the body midline.

Although these differential effects of response cue instructions on the posterior LDAP component are indicative of a contextual modulation of cortical response preparation processes, even more direct evidence for such a top-down bias comes from the pattern of ERP modulations observed in response to task-irrelevant probe stimuli. As can be seen in Figure 5, visual N1 components were generally enhanced when probes were presented on the side that was cued for an upcoming response relative to probes presented on the opposite uncued side. This finding confirms previous observations that covert manual response preparation results in spatially specific modulations of visual processing (Eimer & Van Velzen, 2006; Eimer et al., 2006) and thus provides further evidence that response preparation processes are closely linked to attentional shifts toward response-relevant locations, as postulated by the premotor theory of attention (Rizzolatti et al., 1994). The critical new finding was that such attentional modulations of visual processing are not always confined to locations next to the effector involved in a cued response, but that their locus in external space can instead be shifted by contextual factors. For the group of participants

that were given effector cue instructions (Figure 5, bottom panel), spatially selective effects of response preparation on visual N1 components were reliably elicited when probes were located next to the hands but not when they were presented next to the target keys. This difference might simply be due to the fact that these visual probes were always presented during the covert response preparation interval when hands were still in their resting position. However, the N1 results observed for the group that received direction cue instructions instead (Figure 5, top panel) show that this explanation cannot be correct. For this group, response preparation effects on visual N1 components were only present when probes were presented next to the target location for a cued movement but not when probes were presented next to their starting position, even though hands were still located there. As these spatially selective modulations of visual N1 amplitudes are likely to reflect shifts of attention that are triggered during covert manual response preparation, this pattern of results suggests that such attention shifts are subject to a strong top-down contextual bias. When the importance of effector selection is stressed, the focus of spatial attention remains close to the effector throughout the response preparation interval. In contrast, when the importance of movement direction is emphasized instead, attention is shifted toward the goal location of an anticipated reaching movement well before this movement is initiated.

In summary, the present experiment has found new and compelling evidence for strong top-down contextual biases that are active during response programming and systematically affect the covert preparation of manual reaching movements. These results show that even when full response information is available, sensorimotor processes involved in preparation of motor responses are by no means rigid and automatic but are instead modulated in a top-down fashion by cognitive factors related to expectations, strategies, and the instructed context for a motor task.

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