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Neuroscience Letters 419 (2007) 142–146
Neuroscience Letters
www.elsevier.com/locate/neulet

Covert unimanual response preparation triggers attention shifts to effectors rather than goal locations

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Received 4 February 2007; received in revised form 1 April 2007; accepted 13 April 2007

Abstract

The premotor theory of attention postulates that during response preparation, attention shifts are elicited towards the goal of a prepared movement. Support for this claim comes from research demonstrating enhanced performance at the location of upcoming saccades. To investigate whether attention shifts occur towards effectors or goal locations during the covert preparation of unimanual movements, we recorded event related brain potentials (ERPs) to task-irrelevant tactile probes that were presented while participants prepared to move one hand towards the index finger of the other hand, as directed by visual response cues presented at the start of each trial. These cues specified either the effector or the goal location of an upcoming movement. The somatosensory N140 component was enhanced when probes were presented to the effector hand relative to the goal hand, regardless of cue instructions. Analogous modulations of the N80 component were only present with effector cues. These results demonstrate a close link between covert response preparation and attention shifts, and strongly suggest that attention shifts are directed to the effector, and not to the goal location of manual movements.

Keywords: Unimanual movement preparation; Shifts of attention; Effector hand; Movement goal; Tactile processing; ERPs

The premotor theory of attention [11] suggests that the brain circuits involved in the motor programming of goal-directed movements are also responsible for shifts of covert orienting (i.e., attention shifts without concurrent eye or body movements). Support for this theory comes from research demonstrating enhanced performance to visual, auditory or tactile stimuli at the goal location of a prepared saccade, even before the saccade is executed (e.g. [2,12,13]). While the majority of these studies have investigated links between shifts of attention and oculomotor preparation, attention shifts have also been reported during hand movement preparation [4,8]. For example, we [4] have previously investigated shifts of attention elicited during a delayed hand movement preparation task, where visual cues indicated whether the left or right index finger that was to be lifted after a go signal. Somatosensory ERPs in response to task-irrelevant tactile probes presented during the interval between response cue and subsequent go signal were enhanced when tactile probes were delivered to the finger currently prepared for an anticipated response, relative to tactile probes presented to the uncued hand suggesting that attention shifts are triggered during unimanual response preparation.

In contrast to saccade preparation, which mainly involves goal selection, hand movement preparation also requires the selection of an effector (i.e. right or left hand), with effectors and goals often located in different regions of space. Thus, attention shifts elicited during covert hand movement preparation may be linked to the selection of an effector or of a response goal. This question was not addressed in our previous study [4], as effector and goal locations are always spatially coincident in the case of simple finger lift movements. The aim of the present study was to clarify whether unimanual response preparation triggers attention shifts towards the effector or the goal of an upcoming movement. Participants had to prepare a movement of one hand (as instructed on a trial-by-trial basis by a visual response cue) that was to be executed after a go signal. They had to touch the index finger of the opposite (stationary) hand with the index finger of the cued hand. Because the stationary hand was the goal of a movement that was performed with the other hand, this allowed us to dissociate attentional goal and effector selection during movement preparation.

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0304-3940/$ – see front matter © 2007 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.neulet.2007.04.027

To track any shifts of attention, ERPs were recorded in response to task-irrelevant tactile probes that were presented to the left or right index finger during the response preparation interval. If spatial attention is allocated to the goal of a prepared hand movement, somatosensory ERPs should be enhanced for probes presented to the stationary hand (i.e., the goal of a cued hand movement). In contrast, if attention is allocated to the effector involved in a prepared hand movement, enhanced somatosensory ERPs should be found for probes presented to the effector hand relative to probes presented to the goal hand.

To further explore the possible role of task instructions on attention shifts to effectors versus goals, we ran two separate experimental sessions where the response cues presented at the start of each trial specified either the effector hand that was to be moved or the movement goal (i.e., the stationary hand that was to be touched). In both cases, hand movements were identical. If task instructions affect attention shifts that are triggered during manual response preparation, we should find systematic differences in the attentional bias towards cued effectors or cued goal locations with effector and goal instructions, respectively.

Eight participants (five females and three males) with an average age of 30 years (range of 26–34 years) took part in this study. All participants gave their written informed consent prior to participation. This study was approved by the ethics committee of the School of Psychology at Birkbeck College, and was conducted in accordance with the guidelines set out in the Declaration of Helsinki.

Participants were seated in a dimly lit sound attenuated cabin in front of a computer screen. They placed their left and right hand to the left and right, respectively, of the body midline, with a distance between the index fingers and the body midline of approximately 11 cm. Two solenoids, which drove a metal rod with a blunt conical tip, were attached with medical tape to the top of the middle segment of the index fingers. The rods made contact with the fingers whenever a current (9 V) was passed through the solenoid. Tactile probe stimuli consisted of the rod contacting the finger for 6 ms. White noise (62 dB SPL) was continuously present to mask any sounds made by the tactile stimulators.

Visual cues consisted of two adjacent left-pointing and right-pointing triangles, presented centrally on the computer screen at a viewing distance of 55 cm ($3.5^\circ \times 2.5^\circ$ of visual angle). One triangle was red, the other blue, and they always pointed in opposite directions ('► ◄' or '◄ ►'). Red and blue triangles were presented with equal probability to the left and right side of fixation, or vice versa. A central fixation cross, located between triangles, was continuously present throughout the experimental blocks. Uppercase letters 'G' (Go) and 'S' (Stop), presented at fixation ($0.8^\circ \times 0.9^\circ$ of visual angle), served as Go ('G') and Nogo ('S') stimuli, respectively.

Participants were instructed to prepare one of two manual responses, as indicated by one of the two cue triangles, and to execute or withhold this response following the visual Go/Nogo signal. They were tested in two sessions that were identical except for the task instructions. In one session a participant was instructed that blue triangle cues were task-relevant and indicated which hand needed to be moved on a given trial (effector instruction). In the other session, the same participant was instructed that red triangle cues were now task-relevant and indicated the stationary hand that was to be touched (goal instruction). Four participants completed the first session under effector instructions and the second session under goal instructions, and this order was reversed for the other four participants. The two experimental sessions took place in separate weeks and during debriefing after the second experimental session none of the participants reported being aware of performing the same experiment twice.

In each session, 12 blocks of 96 trials each were run. Each trial started with a 100 ms presentation of the cue, after an interval of 1006 ms this was followed by an imperative stimulus (Go or Nogo). On 80 trials, a tactile probe stimulus was presented with equal probability to the cued and uncued hand, either during the response preparation interval (900 ms after cue onset), or 150 ms after the onset of the imperative stimulus. On the remaining 16 trials, no tactile probe was presented. Participants were instructed to maintain central fixation, to entirely ignore all tactile events, and to move one of their hands as fast as possible in order to touch the bottom segment of the index finger of the other hand in response to the letter 'G' (which was presented on 80 trials per block), but to refrain from responding when the letter 'S' was presented (on 16 trials per block).

Manual response times were measured via an infrared response system consisting of a transmitter and receiver LED located on either side of the middle segment of each index finger in the resting position. A response was registered when the index finger was lifted, allowing the light beam of the transmitter to reach the receiver LED. An error feedback tone (1175 Hz, 50 ms duration) was presented on all trials with either premature responses (hand movements prior to the onset of the Go/Nogo stimulus), responses with the cued goal hand, or without any response within 850 ms after the Go stimulus. These trials were excluded from analysis. The interval between a visual Go/Nogo stimulus and the onset of the response cue on the subsequent trial was 2750 ms. Participant were monitored via a video camera throughout the experiments to ensure that they moved their hand to touch the bottom segment of the index finger of the other hand on each trial. Before the start of each experimental session participants were given half of an experimental block without feedback followed by half of an experimental block with feedback to practise the task.

Continuous EEG was recoded with Ag–AgCl electrodes and linked-earlobe reference from midline electrodes Fpz, Fz, Cz, Pz and Oz, lateral electrodes F7, F3, Fc5, T7, C3, Cp5, P3, P7 (according to the 10–20 system), and from OL (located halfway between O1 and P7) over the left hemisphere and from homologous lateral electrodes over the right hemisphere. Horizontal EOG was recorded bipolarly from the outer canthi of both eyes. Electrode impedance was kept below 5 kΩ, and the impedance of the earlobe electrodes were kept as equal as possible. Amplifier bandpass was 0.1–40 Hz and digitisation rate was 200 Hz. Trials with eyeblinks, horizontal eye movements, or muscle artefacts were excluded prior to data analysis. Trials where tactile probes were presented 150 ms after the onset of the Go/Nogo stimulus were also excluded from data analysis, because some participants had already started to execute the cued hand movement within 150 ms on a substantial number of trials (overall on average on 12% of trials), thereby inducing movement-related artefacts in the ERP data.

Statistical analyses were conducted on the basis of ERP mean amplitudes elicited by tactile probes presented during the covert response preparation interval. ERPs triggered by early tactile probes were averaged relative to a 100 ms baseline prior to tactile stimulus onset for all combinations of instruction (effector versus goal), cue direction (left versus right), and tactile probe location (left versus right). ERP mean amplitudes were computed within latency windows centred on the peak amplitude values of early somatosensory ERP components (N80: 75–95 ms post-stimulus onset; N140: 125–170 ms post stimulus onset). These mean amplitude values were analysed with repeated measures ANOVAs for electrodes FC5/6, CP5/6 and C3/4 over the hemisphere contralateral to the stimulated hand where somatosensory components are maximal. Analyses included the factors: electrode (FC5/6 versus CP5/6 versus C3/4), instruction, cue direction, and tactile probe location. In these analyses, cue direction by tactile probe location interactions indicate a significant modulation of ERP amplitudes to tactile probes presented at the cued versus uncued hand. Greenhouse-Geisser adjustments to the degrees of freedom were applied where appropriate.

Participants failed to execute the cued movement following the go signal on 1.1% of all trials and responded prematurely on 0.4% of trials. Under effector instructions participants responded 10 ms faster when tactile probes were presented to the cued effector (352 ms) compared to the uncued hand (362 ms), and this difference was significant ($t(7) = 3.25$; $p < 0.02$). In contrast, under goal instructions, response times on trials where tactile probes were presented to the uncued effector hand (347 ms) or to the cued goal hand (350 ms) did not differ reliably ($t(7) = 0.57$).

Fig. 1 shows somatosensory ERPs in response to tactile probes delivered to the cued versus uncued hand under effector instructions (left panel) and goal instructions (right panel). Early somatosensory components (N80 and N140) appear strongly affected by response preparation under effector instructions, with enhanced amplitudes when tactile probes were presented to the cued effector hand relative to the uncued goal hand. Under goal instructions, response cueing effects are only present for the N140 component, which is enhanced for tactile probes presented to the uncued effector hand relative to probes presented to the cued response goal hand.

Statistical analysis showed a significant instruction by cue direction by tactile probe location interaction ($F(1/7) = 9.23$; $p < 0.02$) for N80 time window (75–95 ms post-stimulus). Follow-up analysis conducted separately for effector and goal instructions showed a significant cue direction by tactile probe location interaction for effector instructions ($F(1/7) = 28.52$; $p < 0.001$). This confirms that the N80 elicited by tactile probes at the cued effector (i.e., the hand that is being prepared to move) was enhanced in comparison to ERPs elicited by tactile probes at the uncued goal hand. In contrast, no reliable cue direction by tactile probe location interaction was present for N80 amplitudes under goal instructions ($F(1/7) = 1.24$; $p = 0.30$).

For the time window of the N140 component (125–170 ms post-stimulus), significant interactions for instruction by cue direction by tactile probe location ($F(1/7) = 8.55$; $p < 0.03$) and instruction by cue direction by tactile probe location by electrode ($F(2/14) = 6.34$; $p < 0.03$) were present. Follow-up analyses conducted separately for effector and goal instructions showed a significant cue direction by tactile probe interaction ($F(1/7) = 9.67$; $p < 0.02$) under effector instructions. This confirms enhanced N140 amplitudes in response to tactile probes delivered to the cued effector hand compared tactile probes at the uncued goal hand. Under goal instructions, a cue direction by tactile probe location interaction ($F(1/7) = 4.63$; $p = 0.07$) which was close to significance was supported by a significant cue direction by tactile probe location by electrode interaction ($F(2/14) = 5.52$; $p < 0.02$). Further analyses conducted separately for different electrode sites showed a significant cue direction by tactile probe location interaction at C3/4($F(1/7) = 8.58$; $p < 0.03$), where N140 components to tactile probes presented to the uncued effector hand were enhanced relative to ERPs in response to probes presented to the cued goal hand (see Fig. 1, right panel).

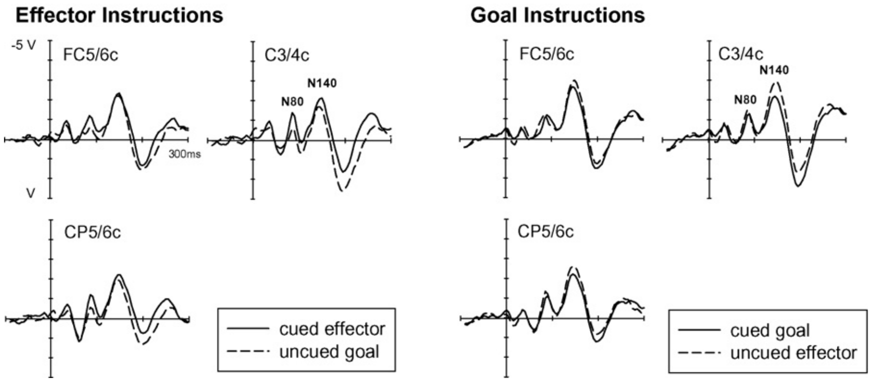

Fig. 1. Grand-averaged somatosensory ERPs elicited by task irrelevant tactile probes in the 300 ms interval following tactile probe onset over the hemisphere contralateral to the stimulated hand close to somatosensory cortex. Left panel: ERPs are shown in response to tactile probes at the cued effector (solid lines) and the uncued goal hand (dashed lines) under effector instructions. Right panel: ERPs are shown in response to tactile probes at the cued goal (solid lines) and the uncued effector hand (dashed lines) under goal instructions.

In the present study, a delayed response preparation task was employed where visual cues indicated either the effector or the goal of an upcoming unimanual hand movement. Participants were cued to move one of their hands (the effector) to touch the other hand (the goal) as quickly as possible after a go signal. Task-irrelevant tactile probes were presented to the effector or the goal hand during covert movement preparation. Somatosensory ERPs to these tactile probes were recorded to investigate whether attention shifts elicited during hand movement preparation are directed towards the effector or towards the goal location for an upcoming movement. As predicted, early somatosensory ERP components (N80, N140) were systematically affected by response precueing. N140 amplitudes were larger when probes were presented to the hand that was to be moved during the anticipated response, relative to probes presented to the opposite hand that served as the movement goal. Notably, this was the case regardless of response instructions (effector versus goal cueing). However, a differential effect of response instructions was observed for the somatosensory N80 component: Only with effector instructions, but not with goal instructions, response preparation resulted in larger N80 components when the cued effector hand was stimulated.

Thus, our results demonstrate that somatosensory processing of tactile probes is enhanced when these are presented to the effector involved in an upcoming movement, but not when probes are presented to the hand that serves as the goal location of this movement. This strongly suggests that shifts of attention elicited during cued unimanual response preparation are at least initially directed towards the effector involved in an upcoming response, and not towards the goal location of this response. Previous electrophysiological studies of tactile spatial attention have repeatedly reported similar modulations of early somatosensory components in response to tactile stimuli presented to the attended versus unattended hand. These studies have found an enhanced negativity in the time range of the N140 component [1,3,5–7,9] but earlier modulations in the time range of the N80 have also been reported [3]. Given these results, the current finding of enhanced N80 and N140 amplitudes for tactile probes delivered to the effector hand involved in an anticipated movement strongly suggest that spatial attention was directed towards this hand (see [4] for similar ERP modulations induced when response cues indicated which hand would be involved in an upcoming simple finger lifting movement). Such links between response preparation and tactile attention might be mediated by parietofrontal circuits that connect somatosensory and motor brain regions, and are involved in sensorimotor transformations during action planning (see [10] for review).

Participants were instructed in one session to interpret the response cues as indicating the effector and in the other session the goal of the next hand movement. Effects related to covert response preparation emerged earlier under effector instructions, where systematic N80 modulations were found, than under goal instructions. In the latter case, response preparation only induced a modulation of the N140 component, analogous to what was also observed under effector instructions. In other words, although somatosensory processing of task irrelevant tactile probes delivered to the effector hand was enhanced regardless of which task instructions was used, such enhancements occurred at an earlier stage of processing when response cues specified effector selection. This suggests that variations of response instructions may have had some impact on the attentional shifts triggered during covert response preparation. Although attention was always directed towards the effector involved in an upcoming movement, these attention shifts may have occurred more rapidly when effector-specific cues emphasized the need to select a specific hand. In contrast, under goal instructions where cues indicated the end location of an upcoming response, the spatial parameters emphasized by the cue may have conflicted with the tendency of attention to be directed towards the effector involved in this response, thereby delaying the onset of spatially specific effects of response preparation on somatosensory ERPs.

Overall, the results of the present study demonstrate the presence of attention shifts that are elicited during unimanual movement preparation. In line with previous studies (e.g. [4,8]), they suggest a close link between the circuits involved in the motor programming of goal-directed movements and circuits involved in covert shifts of attention. Most importantly, the current findings demonstrate that such attention shifts are initially directed towards the effector involved in an upcoming movement, and not to the goal location of this movement.

Acknowledgments

This research was supported by a grant from the Biotechnology and Biological Sciences Research Council (BBSRC). M.E. holds a Royal Society-Wolfson Research Merit Award.

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