Motor Planning Is Facilitated by Adopting an Action's Goal Posture: An fMRI Study

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Motor planning is a hierarchical process that is typically organized around an action's goal (e.g., drinking from a cup). However, the motor plan depends not only on the goal but also on the current body state. Here, we investigated how one's own body posture interacts with planning of goal-directed actions. Participants engaged in a grasp selection (GS) task while we manipulated their arm posture. They had to indicate how they would grasp a bar when transporting it from a start to goal position and orientation. We compared situations in which one's body posture was incongruent with the start posture and/or goal posture of the planned movement. Behavioral results show that GS took longer when one's own body state was incongruent with the goal posture of the planned movement. Correspondingly, neural activity in the intraparietal sulcus (IPS) and extrastriate body area (EBA) was modulated by congruency between the body state and the action plan. IPS was sensitive to overall congruency between body posture and action plan, while the EBA was sensitive specifically to goal posture congruency. Together, our results suggest that IPS maintains an internal state of one's own body posture, while EBA contains a representation of the goal posture of the action plan.

Keywords: action simulation, EBA, movement representation, parietal, premotor

Introduction

Action plans are typically specified at a high symbolic level, such as taking a sip from a cup of tea (Wolpert and Ghahramani 2000). Yet, there is almost an infinite amount of solutions by which this action plan could be achieved. Finding a good solution is a fundamental decision process that depends on both the current state of our body and the context at hand (Kording and Wolpert 2006).

One fundamental organizational principle that has emerged is that action plans are organized in a hierarchical fashion around temporally distal outcomes or goals (Rosenbaum et al. 2001; Grafton and Hamilton 2007; Kilner et al. 2007). Behavioral studies have shown that motor properties (such as grip force and size and movement speed) are adjusted on the basis of the final action goal (Gentilucci et al. 1997; Rosenbaum et al. 2001). As an everyday example, picking up a glass with the goal to drink from the glass results in a different grasp pattern (thumb pointing up) than picking up the glass with the goal to put it upside down (thumb pointing down). Also, neurophysiological studies suggest that the parietal and precentral cortex may be organized in terms of action goals and spatial locations to which the hand is directed (Graziano et al. 2002; Cooke et al. 2003; Stepniewska et al. 2005) rather than simply representing movements or muscles.

Motor cognition can be facilitated or impaired by changing one's own physical body posture. For example, judging the plausibility of a particular action is more difficult when one's own body posture is incongruent with the action (Sirigu and Duhamel 2001). Also, reaction times (RTs; Parsons 1994; Shenton et al. 2004) and neural activity in the posterior parietal cortex (de Lange et al. 2006; Pellijeff et al. 2006; Parkinson et al. 2010) are larger when participants (implicitly) have to plan actions that are incongruent with their current physical body posture. In this study, we make use of this postural congruency effect to examine whether action plans are elaborated around goal postures. We established a new task that allows us, in contrast to previous experiments, to distinguish between effects caused by congruency between body posture and a movement's start posture and those caused by congruency between body posture and a movement's goal posture. If action plans are organized around goal postures, we expect that action planning is facilitated when a participant's physical body posture is congruent specifically with its goal posture. Alternatively, action planning could also be facilitated when subjects adopt the start posture of the to-be-planned movement. We tackled this question by presenting participants with a cylindrical bar (see Fig. 1), which had to be grasped and transported from its center cradle to either the left or the right cradle (Rosenbaum et al. 1990). We asked subjects how they would grasp the bar, if they would carry out the instructed movement. We manipulated the physical posture of participants' body, in order to probe whether action planning facilitation occurs as a function of participants' physical posture. Furthermore, we measured neural activity using functional magnetic resonance imaging (fMRI) to probe the neural mechanisms of this facilitation process as a function of congruency between physical body posture and goal posture of the action plan. Previous studies have identified 2 brain regions that potentially contain body representations for use in motor control: the intraparietal sulcus (IPS) located within the posterior parietal cortex and the extrastriate body area (EBA). Neuroimaging (Johnson et al. 2002; de Lange et al. 2006; Pellijeff et al. 2006; Parkinson et al. 2010) and neuropsychological (Wolpert et al. 1998; Jackson et al. 2005) studies suggest a role for the IPS in maintaining an internal representation of one's physical body state. This body state is thought to be estimated based on both incoming sensory information and efference copies of motor commands (Wolpert and Ghahramani 2000). Similarly, the EBA is thought to contain a visual representation of the body (Downing et al. 2001), which, importantly, is also called upon during action planning and execution (Astafiev et al. 2004; Helmich et al. 2007; Kuhn et al. 2011). Therefore, we expect neural activity in these areas to be modulated by the mismatch between one's own physical body state and the body states during the elaboration of the motor plan.
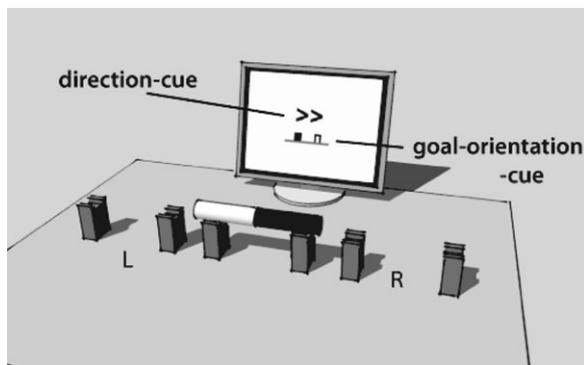
Figure 1. ME task. A cylindrical bar is placed on the center cradle. Trial instructions are provided on the screen. In the example, the instructions require the subject to place the bar on the right cradle (R), as indicated by the direction cue and with the black end to the left, as indicated by the goal-orientation cue. In this example, a rotation of the bar is required.

Material and Methods

Participants

Twenty participants (13 females) with an average age of 23 ± 2 (mean ± standard deviation [SD]) years participated after giving informed consent according to institutional guidelines (CMO region Arnhem-Nijmegen, the Netherlands) for payment of 10 euros/h or course credit. All subjects were consistent right-handers and had normal or corrected-to-normal vision. Due to technical issues, we did not collect behavioral data from 2 participants during the motor execution (ME) task and from 1 participant during the grasp selection (GS) task. Two participants were excluded from the analysis because of idiosyncratic performance on both ME and GS tasks (defined by >2.5 SD from mean).

Experimental Paradigm

Participants first engaged in a ME task, during which we recorded movement profiles. Subsequently, participants engaged in a GS task, during which we acquired behavioral data and fMRI data.

ME Task

Three cradles were positioned on a table next to each other at 5 cm distance between adjacent cradles (Fig. 1). We instructed participants to grasp a bar (length: 25 cm, diameter: 2.5 cm) that was positioned on the middle cradle using a power grip and place it according to instructions presented on a screen. One half of the bar was black, whereas the other half was white. The instruction involved both a direction (i.e., whether to place the bar on the left or right cradle) and a goal orientation of the bar (i.e., where the white and black end of the bar are pointing).

Some actions required a simple translation of the bar from the middle cradle to the left or right cradle, whereas other actions required a 180° rotation. We also included trials in which the bar had to be placed vertically (requiring a 90° rotation), allowing for comparison with earlier studies (Rosenbaum et al. 1992). We instructed participants to position their own hand on the table prior to every trial with the palm facing either up or down. We changed body posture prior to each block of 8 trials. During the ME task, we tracked participants' hand position using a 3D motion tracking device (Polhemus Liberty, Colchester, USA) using 2 sensors at the left and right edge of the wrist of the right arm and a sampling frequency of 240 Hz. Movement times and grip choice were calculated from these recordings. Subjects engaged in 5 training trials and 96 ME trials (32 trials involving translation, 32 trials involving rotation, and 32 trials involving vertical placement), lasting ~20 min.

GS Task

Immediately after the ME task, participants engaged in a GS task, while whole-brain activity was measured using fMRI. During the GS task,

participants were presented with a drawing of a bar on the center cradle, representing the start configuration. We used the same instructions to signal the desired goal direction (left or right) and orientation (where the white and black end of the bar were pointing), as illustrated in Figure 2. The crucial difference between tasks was that in the GS task we asked our participants to report "where they would place their thumb on the bar" in order to move the bar from starting to goal position. They indicated whether they would place their thumb on the black or white end of the bar, using 1 of 2 buttons with their index and middle finger of their left hand. We established RTs and grip choice from these button box responses.

Prior to each block of 8 trials, we manipulated participants' right arm posture, by instructing participants to position their right hand in a palm up or palm down orientation. Note that no overt movements had to be performed during the GS task, and hand posture therefore did not change during a trial. The posture manipulation resulted in different patterns of congruency between subject's own hand posture and the hand posture(s) during the planning task. During trials requiring no bar rotation but only bar translation (TRANSLATION trials), participants' posture could either be "overall congruent" or "overall incongruent" with the planned action (because the start posture and goal posture are the same for these actions, see Fig. 2A). During trials requiring a bar rotation (ROTATION trials), participants' posture could either be in a "start-posture congruent/goal-posture incongruent" posture or "start-posture incongruent/goal-posture congruent" posture with the planned action. Note that in ROTATION trials, a "start-posture congruent" posture is automatically "goal-posture incongruent" (because the action involves a rotation, start posture and goal posture are necessarily opposite, see Fig. 2B). During trials requiring 90° bar rotation (VERTICAL ending trials), participants' posture could either be "start-posture congruent" or "start-posture incongruent," while always being incongruent with the goal posture (because we never asked participants to keep their hand in a thumb-up or -down orientation, see Fig. 2C).

Participants engaged in 15 practice trials outside the scanner and 40 practice trials inside the fMRI environment. Then, participants engaged in 320 trials (120 trials involving translation, 120 trials involving rotation, and 80 trials involving vertical placement). Trials were divided in 5 blocks of each 64 trials, with rest breaks in between blocks. Trials were presented in pseudorandom order such that each block contained the same number of trials of each condition, and the same instruction cue was not presented twice in a row.

Each trial began with a picture showing only the bar resting on the central cradle, representing the start configuration of the ME task. After a 1-s delay, the instruction cue appeared and was shown, together with the picture of the bar, for 3 s. Appearance of the instruction cue was taken as trial onset for further analysis of behavioral and neuroimaging data. Following this there was a jittered intertrial interval of 2.5–4.5 s.

Scanning was split in 2 sessions, each of which lasted ~25 min. There was a short break (<2 min) between the sessions. Participants remained inside the scanner during the break.

Analysis of Kinematic and Behavioral Data

During the ME task, we used a minimum-speed approach to obtain initiation, grasp, and movement times. Initiation time (IT) was defined as the time when participants started to move. Grasp time (GT) was defined as the time when participants lifted the bar from the middle cradle. Movement time (MT) was defined as the time between the first movement of the hand and the time when hand velocity was lowest within a 10 × 5 × 5 (width, depth, height) cm range of the target cradle (i.e., when the goal was achieved). Hand orientation at the moment of grasping and placing was obtained from the relative position of the motion sensors. On the basis of this, trials in which subjects did not follow the instructions were removed (on average, 4.2% of the trials were removed by this procedure). The bar could be grasped using either an overhand (prone) or an underhand (supine) grip. We defined grip preference as the ratio of underhand grips used for a particular trial type. In order to probe the effect of action complexity on performance, we analyzed IT, GT, MT, and grip preference as a function of trial type (rotation, translation, vertical) using a one-way analysis of variance (ANOVA).
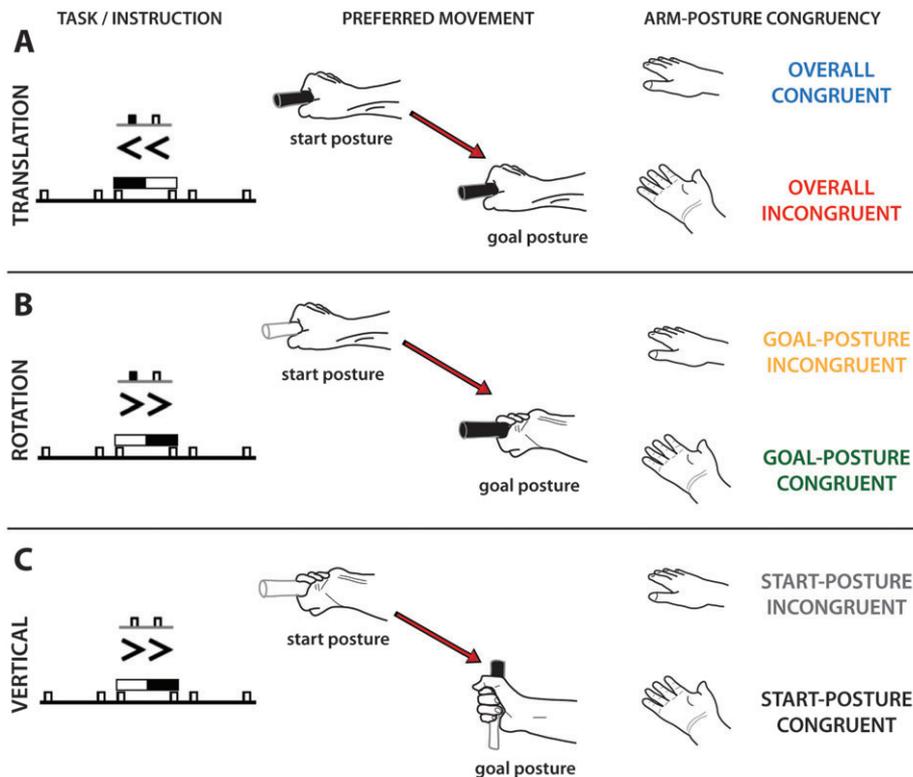
Figure 2. GS task. Stimuli and conditions of GS task with translation (*A*), rotation (*B*), and vertical (*C*) trials. Left column shows example stimuli (compare Fig. 1). Middle column shows preferred start posture and goal posture during the movement. Right column shows the participant's possible arm postures, as well as how these result in (in)congruency between body posture and posture(s) of the planned movement.

RTs and grip preference during the GS task were obtained using the button box responses. Trials with RTs exceeding 2 SDs above a participant's condition mean were removed from analysis. On average, 8.4% of the trials were removed by this procedure (the majority of removed trials was from the early phase of the experiment, suggesting that some participants had not yet fully learnt the trial contingencies at the start of the experiment).

To compare performance between ME and GS, we compared movement and RTs and grip preferences between ME and GS for all possible movements (3 movement types (rotation, translation, vertical) × 2 positions (left, right) × 2 body postures (palm up, palm down)), using Spearman correlations.

In order to probe the effect of action complexity on performance, we analyzed RTs and grip preference as a function of trial type (rotation, translation, vertical) using a one-way ANOVA. We assessed postural congruency effects separately for each trial type. For TRANSLATION trials, we compared RTs for trials with overall congruent and trials with overall incongruent body posture. For ROTATION trials, we compared RTs for trials where participants own posture was incongruent with the goal posture and trials where the own posture was congruent with the goal posture of the action plan. For VERTICAL trials, we compared trials where participants own posture was congruent with the start posture and trials where it was incongruent with the start posture. We used one-tailed paired samples t-tests for these comparisons.

Image Data Acquisition

We used a 1.5-T Avanto MR-scanner (Siemens, Erlangen, Germany), using a 32-channel head coil for signal reception to acquire whole-brain T_2^*-weighted gradient-echo echo-planar images (time repetition [TR]/time echo [TE] = 2140/40 ms, voxel size 3.5 × 3.5 × 3.5 mm). For each participant, we collected a total of ~1400 volumes in 2 sessions. The first 5 volumes of each session were discarded to allow for T_1 equilibration effects. Anatomical images were acquired with a T_1-weighted magnetization prepared rapid gradient-echo sequence (TR/

TE = 2250/2.95 ms, voxel size 1 × 1 × 1 mm). The head of each participant was carefully constrained using cushions on both sides of the head and participants were instructed to remain as still as possible during the experiment. Inspection of the data showed that there were no excessive head movements in any of the participants.

Imaging Data Analysis

Imaging data were analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). First, functional images were spatially realigned using a sinc interpolation algorithm that estimates rigid body transformations (translations, rotations) by minimizing head movements between each image and the reference image (Friston, Ashburner, et al. 1995). Subsequently, the time series for each voxel was realigned temporally to acquisition of the first slice. Images were normalized to a standard EPI template centered in Talairach space (Ashburner and Friston 1999) by using linear and nonlinear parameters and resampled at an isotropic voxel size of 2 mm. The normalized images were smoothed with an isotropic 8-mm full-width at half-maximum Gaussian kernel. Anatomical images were spatially coregistered to the mean of the functional images and spatially normalized by using the same transformation matrix applied to the functional images. The ensuing preprocessed fMRI time series were analyzed on a subject-by-subject basis using an event-related approach in the context of the General Linear Model. For each trial type, square wave functions were constructed with a duration corresponding to the mean RT of the subject and convolved with a canonical hemodynamic response function and its temporal derivative (Friston, Holmes, et al. 1995). Finally, the statistical model included separate regressors of no interest, modeling the period in which the subject changed posture, incorrect and missed responses, residual head movement-related effects, and low-frequency signal drifts over time. Parameter estimates for all regressors were obtained by maximum-likelihood estimation, using a temporal high-pass filter (cutoff 128 s), and modeling temporal autocorrelation as an AR(1) process. Linear contrasts pertaining to the main effects of the factorial design were calculated.

We specifically compared TRANSLATION trials, in which body posture could be overall congruent or overall incongruent, ROTATION trials, in which body posture could be congruent or incongruent to the action's goal posture, and VERTICAL trials, in which body posture could be start-posture congruent or start-posture incongruent. Contrasts of the parameter estimates for these comparisons constituted the data for the second-stage analyses, which treated participants as a random effect (Friston et al. 1999). Additionally, we included the behavioral effect size of each contrast for each participant as a covariate in the analysis.

Statistical Inference

We isolated regions that were sensitive to complexity of the action plan by looking for regions that exhibited differential activity between ROTATION and TRANSLATION trials. Furthermore, we investigated how postural congruency affected neural activity by comparing: 1) trials with overall congruent and overall incongruent body posture for TRANSLATION trials (contrast: overall incongruent body posture – overall congruent body posture); 2) trials with goal-congruent and goal-incongruent body posture for ROTATION trials (contrast: goal-posture incongruent body posture – goal-posture congruent body posture); and 3) trials with start-congruent and start-incongruent body posture for VERTICAL trials (contrast: start-posture incongruent body posture – start-posture congruent body posture). We used paired samples t-tests for these comparisons.

Statistical inference was performed using a cluster-level statistical test to assess clusters of significant activation (Friston et al. 1996). We used a corrected cluster threshold of $P < 0.05$, on the basis of a threshold of $P < 0.001$ at the voxel level at the whole-brain level. Additionally, we used a priori anatomical information from previous studies to constrain our search space (Friston et al. 2006) to 2 regions that have been consistently involved in arm and body representation during action planning: the IPS and the EBA. We defined search volumes comprising spheres of 10 mm around these regions (IPS: [–25, –56, 56], de Lange et al. 2006; EBA: [–51, –72, 8], Downing et al. 2001) and corrected our results for multiple comparisons using a familywise error rate (FWE) threshold of $P < 0.05$ within this search volume (Worsley 1996).

Anatomical details of significant signal changes were obtained by superimposing the statistical parametric maps on the structural images of the subjects. The atlas of Duvernoy et al. (1991) was used to identify relevant anatomical landmarks.

Results

Behavioral Results—ME Task

We obtained IT, GT, and MT, as well as grip preference measures during the ME task. ITs were longer for trials that required a 180° rotation of the bar (ROTATION trials, 1012 ms) than for trials that required a 90° rotation (VERTICAL trials, 909 ms) and trials that did not require any rotation (TRANSLATION trials, 950 ms; e.g., see Fig. 2) ($F_{2,30} = 6.36$, $P = 0.005$). Post hoc analyses (paired samples t-tests) revealed that ITs were significantly longer for ROTATION than VERTICAL ($t_{15} = 2.57$, $P = 0.011$) and TRANSLATION trials ($t_{15} = 2.73$, $P = 0.008$). GTs behaved similar as ITs, while MTs differed in the sense that participants had longer MTs for VERTICAL compared to TRANSLATION trials.

Based on previously established comfort ratings for different postures (Rosenbaum et al. 1992), we assessed whether predicted grip preference for a particular action sequence corresponded with the actual grip preference of participants in the ME task. Indeed, grip preferences during ME strongly correlated with expected grip preferences ($r = 0.94$, $P < 0.001$), in line with models of end-state comfort (Rosenbaum et al. 2001).

Behavioral Results—GS Task

We collected RT and grip preference measures during the GS task. RTs differed between the 3 movement types ($F_{2,32} = 15.28$, $P < 0.001$), specifically, RTs for ROTATION trials (2198 ms) were longer than for VERTICAL trials (1984 ms; $t_{16} = 2.27$, $P = 0.19$) and TRANSLATION trials (1792 ms; $t_{16} = 6.76$, $P < 0.001$).

When directly comparing RTs during the GS task with planning and execution times (i.e., IT, GT, and MT) of executed movements for corresponding action plans, there were strong correlations between RT and each of these parameters (r(RT,IT) = 0.55, $P = 0.015$; r(RT,GT) = 0.53, $P = 0.019$;
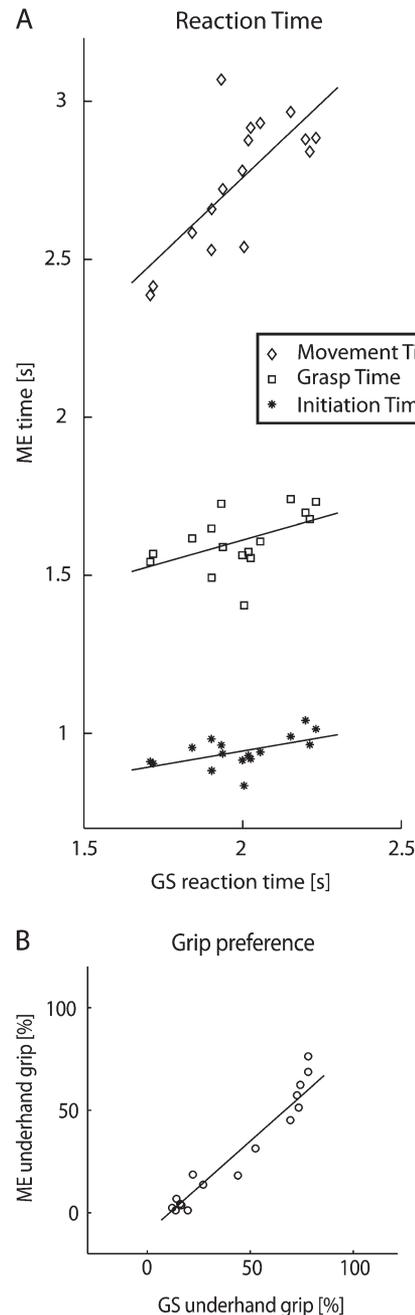

Figure 3. Comparison of behavioral performance during ME and GS task. Average ITs, GTs, and MTs (A, in seconds) and grip preference (B, proportion underhand grips) during ME for all possible movements are highly similar to average RTs and grip preference during GS for corresponding movement types.

$r(RT,MT) = 0.70$, $P = 0.002$; Fig. 3A). Moreover, indicated grip preference during the GS task correlated strongly with the observed grip preference during the ME task ($r = 0.97$, $P < 0.001$, Fig. 3B). They also correlated strongly with predicted grip preferences ($r = 0.857$, $P < 0.001$), based on previously described comfort ratings (Rosenbaum et al. 1992). Together, these data indicate that the duration and outcome of cognitive processes during the GS task are highly similar to those observed during actual motor preparation and execution.

Behavioral Results—Effect of Hand Posture

We next assessed the effect of hand posture on RT during the GS task. During TRANSLATION trials, participants' posture could either be overall congruent or overall incongruent with the planned action (because the start posture and goal posture are the same for these actions, see Fig. 2). Participants were faster with their hand in an overall congruent posture than in an overall incongruent posture (difference = 93 ms: $t_{16} = 3.15$, $P = 0.003$, Fig. 4, top). During ROTATION trials, participants' posture could be either congruent or incongruent with the goal posture of the planned action (because the action involves a rotation, start posture, and goal posture are necessarily opposite). Here, participants were faster when their hand was in a goal-posture congruent compared to a goal-posture incongruent posture (difference = 54 ms: $t_{16} = 2.17$, $P = 0.023$, Fig. 4, middle). During VERTICAL ending trials the posture manipulation had no effect on RTs ($t_{16} = 0.05$, $P > 0.10$, Fig. 4, bottom), that is, they were equally fast no matter whether their own posture was congruent or incongruent to the start posture of the planned movement.
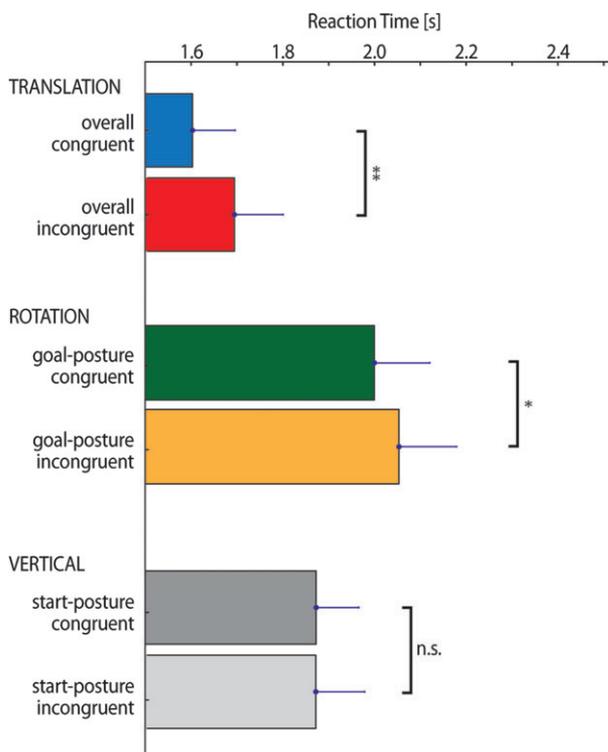
Neural Activity—Movement Complexity

When comparing trials of different movement complexity (ROTATION > TRANSLATION) during GS, we observed increased activity in parietal and premotor cortex (Fig 5A,B). In the premotor cortex, we observed a dorsal and ventral cluster of activation. The dorsal premotor cluster (PMd) falls within the probability range (50%) of Brodmann Area (BA) 6 (Eickhoff et al. 2005). The ventral premotor cluster (PMv) overlaps with both BA 6 (30–70%) and BA 44 (30–60%). The intraparietal activation cluster falls within the probability range (40–90%) of BA 7a. A correlation analysis showed that there was a tight link between intersubject variability in RT difference between ROTATION and TRANSLATION trials on the one hand and neural activity difference between these conditions in this network on the other hand. This is illustrated for the left IPS in Figure 5C. A complete list of activated brain regions, including the correlation with intersubject RT differences, can be found in Table 1.
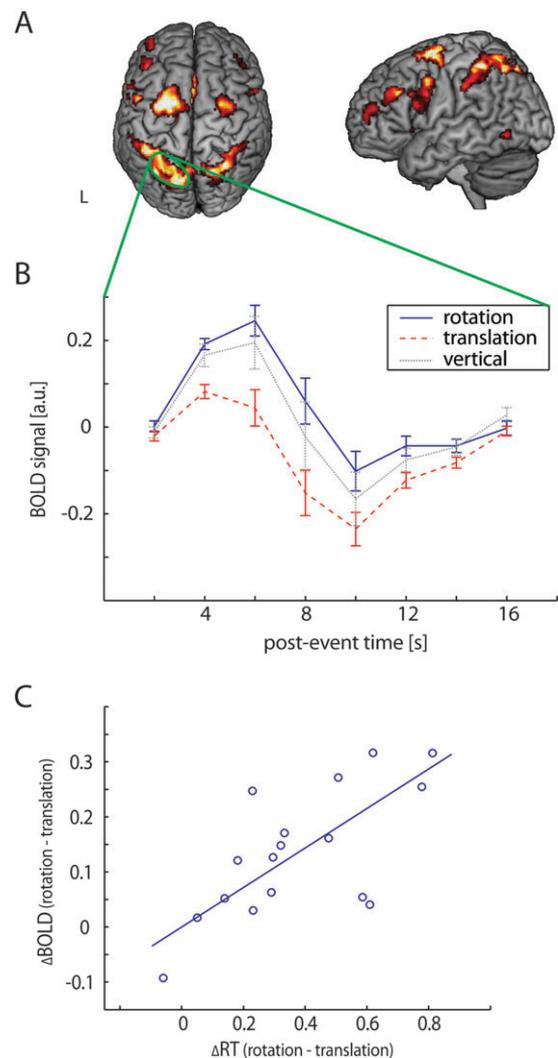
Figure 5. Neural activity modulated by complexity of movement plan. (A) Brain rendering showing areas that were significantly more activated as a function of movement complexity during the GS task (rotation > translation, thresholded at $T > 4$ for display purposes). (B) Event-related response of left IPS (box), plotted for different levels of complexity of the movement plan. (C) Correlation between BOLD and RT differences of each subject between rotation and translation trials. For details on conditions and color coding, see Figure 2.

Figure 4. Behavioral performance during GS task. Plotted are averages of planning times for different movement types (translation [top], rotation [middle], vertical [bottom]) as well as effects of posture congruency on each movement type. For detailed description and color coding of conditions, see Figure 2.

Table 1

Summary of brain regions more strongly activated during (complex) rotation trials compared with (simple) translation trials

Anatomical region	Local maxima			t-Value	Cluster size	P cluster	r (ΔBOLD, ΔRT) (P)
L precentral gyrus	−28	−2	62	13.15	4615	<0.001	**0.60 (0.013)**
L middle frontal gyrus	−28	0	50	11.74			
L superior medial gyrus	−18	0	64	11.29			
L superior parietal lobe	−24	−60	54	9.37	6358	<0.001	**0.68 (0.003)**
R superior parietal lobe	24	−60	58	10.12			**0.70 (0.002)**
L precuneus	−10	−68	54	10.63			
L middle occipital gyrus	−24	−62	32	9.57			
L inferior parietal lobe	−42	−44	55	9.36			
L middle frontal gyrus	−42	28	32	7.60	410	<0.001	**0.65 (0.004)**
L middle frontal gyrus	−40	38	30	5.62			
L middle frontal gyrus	−38	52	16	5.43			
L insula	−28	24	2	6.31	281	<0.001	n.s.
R inferior frontal gyrus	34	24	10	6.10	374	<0.001	n.s.
R insula	36	22	0	5.82			
L inferior temporal lobe	−46	−64	−6	6.02	180	<0.001	**0.60 (0.011)**
L middle temporal lobe	−44	−58	4	5.07			
R precentral gyrus	56	10	30	5.62	85	0.026	n.s.
L thalamus	−8	−12	8	5.18	80	0.034	*0.47 (0.058)*
R middle frontal gyrus	36	28	32	4.91	98	0.013	n.s.
R inferior frontal gyrus	38	30	28	4.29			

Note: For clusters that span several anatomical regions, more than one local maximum is given. Cluster size is given in number of voxels. All clusters are significant when correcting for multiple comparisons across the whole brain. For each cluster, the correlation coefficient (and corresponding P value) of the intersubject BOLD and RT differences is given. Correlation coefficients are printed in bold letters for significant correlations, and in italic letters for trends. n.s., not significant; L, left; R, right.

Since our group comprised both male and female participants, we carried out a control analysis to assess the generality of the observed neural activity difference. This analysis showed that the activity difference was present in both male and female participants, with no significant differences between groups (Supplementary Fig. 1).

Neural Activity—Effect of Hand Posture

During TRANSLATION trials, we observed increased neural activity in the left IPS ([−22, −60, 58]; $T = 4.39$, $P_{FWE} = 0.019$) and right IPS ([20, −68, 58]; $T = 4.35$, $P_{FWE} = 0.018$) when subject's hand posture was overall incongruent with the planned action (Fig. 6A,B). Moreover, interindividual differences in blood oxygen level–dependent (BOLD) activity between congruent and incongruent posture conditions correlated with differences in RTs between postures in the left IPS ($r = 0.531$, $P = 0.028$; see Fig. 6C) and right IPS ($r = 0.539$, $P = 0.026$).

An exploratory whole-brain search for significant differences yielded no other significant activation differences.

During ROTATION trials, we observed increased neural activity in the EBA ([−42, −72, 10]; $T = 5.48$, $P_{FWE} = 0.001$) when participants adopted a goal-incongruent hand posture compared with goal-congruent hand posture (Fig. 7A,B). This increased neural activity was not significantly related to interindividual differences in RTs between postures ($r = −0.149$, $P > 0.10$).

There were no significant activation differences on the whole-brain analysis.

Manipulation of hand posture did not result in larger neural activity during VERTICAL trials. For a summary of all activity differences related to posture, see Table 2.

Discussion

In this study, we investigated how one's own body posture interacts with planning of goal-directed actions. Behavioral
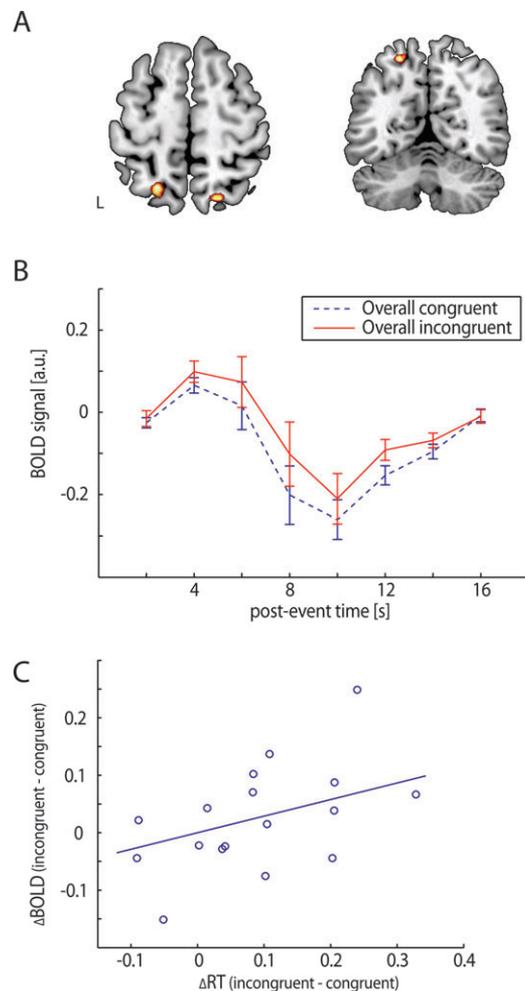
Figure 6. Neural activity modulated by overall body posture congruency. (A) Anatomical localization of areas that were more active when body posture was overall incongruent with the movement plan during the GS task (thresholded at $T > 2$ for display purposes). (B) Event-related response of left IPS, plotted for different levels of body posture congruency. (C) Correlation between BOLD and RT differences of each subject between congruent and incongruent posture. For details on conditions and color coding, see Figure 2.

results indicate that motor planning is facilitated when one's own body state is congruent with the goal posture of the planned movement. fMRI results show that 2 regions, the IPS and EBA, showed an interaction between body posture and action planning. There was more activity in IPS when the body posture was overall different from those that were calculated for the action plan. EBA was more active when the body posture was incongruent with the goal state of the planned action than when they were congruent. Together, our results indicate that movement planning is facilitated (in terms of behavioral performance and neural computation) by adopting the goal posture of the movement, in line with models that hypothesize that movement planning is organized around the specification of goal postures (Rosenbaum et al. 2001; Graziano et al. 2002).

Importance of Goal Posture in Movement Planning

When participants decided how to grasp the bar, they predominantly selected the option that resulted in a comfortable goal posture. This finding replicates earlier work using
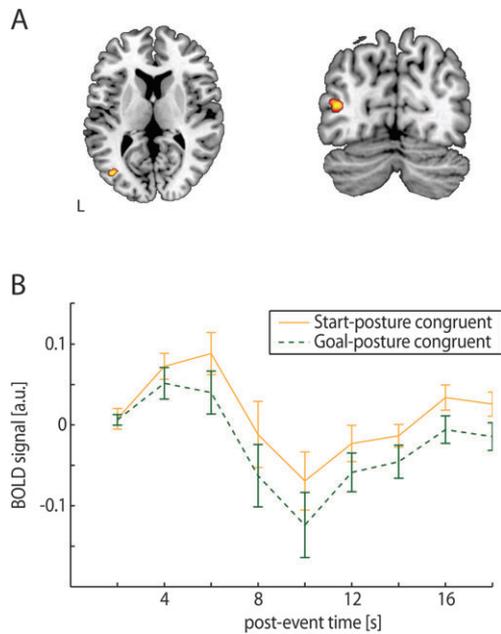
Figure 7. Neural activity modulated by goal-posture congruency. (A) Anatomical localization of areas that were more active when body posture was incongruent with the goal posture of the movement plan during the GS task (thresholded at $T > 2$ for display purposes). (B) Event-related response of left EBA, plotted for different levels of body posture congruency. For details on conditions and color coding, see Figure 2.

a similar experimental setup (Rosenbaum et al. 1990, 1992) and suggests that during motor planning the solution to the selection problem is determined on the basis of the goal state of an action. We extend these observations by showing that planning of movements is facilitated when proprioceptive information about one's own body state is congruent with the movement's goal state. Thereby, our behavioral results are in good accord with theories that posit that movement planning is organized around goal postures (Rosenbaum et al. 1995, 2001; Weiss et al. 2007).

Parietal and Premotor Cortex Are Modulated by Movement Complexity

The GS task activated a parietal–premotor network comprising the superior parietal, as well as dorsal and ventral premotor cortex. The involvement of superior parietal and dorsal premotor cortex (PMd) during the elaboration of motor plans is in line with previous studies of movement planning in monkeys (Kalaska et al. 1997; Scott et al. 1997) and humans (Beurze et al. 2007). The involvement of ventral premotor cortex (PMv) also fits well with earlier findings on "canonical neurons" in both monkeys (Murata et al. 1997; Joly et al. 2009) and humans (Grezes, Armony, et al. 2003). These neurons are selectively activated both by the presentation of specific objects and their corresponding motor program (Rizzolatti and Luppino 2001). We show that activity within this network increased with increasing complexity of the movement plan, from a simple translation to combined translation and rotation movements. A highly similar linear relationship between movement complexity and neural activity in this network has been previously observed during mental rotation of body parts (Parsons et al. 1995; Richter et al. 2000; de Lange et al. 2005, 2006), suggesting that the underlying neuronal computations may be similar. In particular, both motor planning and mental

rotation of body parts may involve a process of alignment of the actual and desired hand postures.

Individual differences in motor planning demands (as indexed by RTs) correlated with neural activity differences within this network. The strong link between behavioral and neural data suggests that the larger neural computations in this parietal–premotor network are a direct neural corollary of the longer planning times as movement complexity increases. Therefore, the activation differences are related to differences in the strength of the hemodynamic response (rather than its presence or absence). This is supported by the hemodynamic response plots in Figures 5-7, which show BOLD responses for all conditions in the brain areas of interest. Along this line, we interpret stronger activation in one condition compared with another as reflecting more intense/prolonged processing within that brain area, whereas reduced activity indexes a relative facilitation of neural computation in the brain area.

Incongruence between Body Posture and Action Plan Leads to Larger Activity in Intraparietal Sulcus and Extrastriate Body Area

There were 2 regions whose activity was modulated by participant's body posture during the movement planning task: IPS and EBA. Interestingly, both IPS (Wolpert et al. 1998; Jackson et al. 2005; Pellijeff et al. 2006; Parkinson et al. 2010) and EBA (Downing et al. 2001; Astafiev et al. 2004; Saxe et al. 2006; Kuhn et al. 2011) appear to contain a representation of the body. In our study, IPS showed increased activity when one's arm posture was overall different from the posture used in the motor plan (i.e., with both the start and the goal posture of the movement). EBA, on the other hand, showed increased activity specifically when one's arm was different from the goal posture of the planned action. In the following sections, we will discuss potential functions of both areas during the generation of a motor plan.

Estimation of Body State in Posterior Parietal Cortex

We observed increased activity in the posterior parietal cortex when there was an incongruence between one's arm posture and the arm posture of the action plan. The posterior parietal cortex integrates sensory information from multiple modalities with information pertaining to the motor plan from efference copies (Andersen and Cui 2009). These sources of information are used to generate an estimate of a body state, in order to achieve an accurate representation of the current body state (Wolpert and Ghahramani 2000; Grush 2004; Pellijeff et al. 2006; Parkinson et al. 2010). Therefore, the increased activation in the posterior parietal cortex for incongruent postures suggests that this region may in fact be engaged with 2 (closely related) processes: maintaining an internal representation of one's physical body and calculating the (simulated) body state during the planned action. This is compatible with earlier studies on mental simulation of reaching (de Lange et al. 2006) and grasping movements (Grezes, Tucker, et al. 2003; Vargas et al. 2004), which observed larger activity in posterior parietal and premotor cortices when a simulated body state does not match one's current body state. Perhaps somewhat surprisingly, IPS was not differentially modulated by body posture during rotation movements, in which participants adopted either a goal-congruent or a goal-incongruent (i.e., start-posture congruent)

Table 2
Posture congruency effects during the motor planning task

Contrast	Anatomical region	MNI coordinates			Cluster size	t-Value
		x	y	z		
Incongruent > congruent overall posture (translation trials)	IPS	−20	−60	58	14	4.39
		20	−68	58	20	4.35
	Precentral gyrus	−10	−24	56	14	4.51
	Inferior frontal gyrus	−38	24	22	13	4.49
	Caudate nucleus	22	26	6	11	5.43
Incongruent > congruent goal posture (rotation trials)	**Middle occipital gyrus (EBA)**	−42	−72	2	54	5.48
	Fusiform gyrus	30	−64	10	17	4.76
	Superior medial gyrus	2	46	46	34	5.99
	Postcentral gyrus	−48	−30	61	13	4.61
	Postcentral gyrus	−62	−12	20	27	4.23
	Postcentral gyrus	66	−22	20	12	3.91

Note: Activity differences in the areas in bold font are based on an analysis within an a priori search space and survived multiple comparisons correction. Activity differences in the other listed areas were significant at a lenient threshold of $P < 0.001$ uncorrected but did not survive correction for multiple comparisons. Therefore, these areas are solely listed for reference. Cluster size is given in number of voxels. MNI, Montreal Neurological Institute.

body posture. We speculate that the absence of activation differences may be related to the fact that congruent and incongruent phases cancel out each other in these action plans. That is, a start-congruent posture is initially congruent but later incongruent with one's body posture and vice versa when body posture is congruent with the goal posture. While this could induce a temporal difference in IPS activity between these conditions, this may be too small to be detected using the sluggish hemodynamic response.

The posterior parietal cortex receives information from various parts of the cortex, including motor and premotor areas on the one hand, and vestibular cortex and areas involved in visual processing on the other hand (Bakola et al. 2010). Based on this connection pattern, Bakola et al. suggested that the superior parietal lobe processes information about limb postures and may play a role in coordinated limb movements in the environment. This information is necessary to enable the comparison of perceived and estimated limb positions in the posterior parietal cortex. One possible mechanism to incorporate contextual information in motor plans has been proposed by Gail et al. (2009). They observed gain modulation by behavioral context in the parietal reach region, located on the medial bank of IPS, in an antireach task and suggest that gain field modulations enable flexible goal-directed behavior. In line with this, gain field modulations by the current body posture (i.e., its state estimate) may underlie the increased activation in IPS observed in the current study.

The posterior parietal cortex has not only been associated with movement planning prior to execution but also with fast online corrections of ongoing movements. Desmurget et al. (1999) showed that disruption of neural processing in PPC by TMS impairs the ability of healthy subjects to update and correct ongoing movements to visual targets. This disruption, in our view, may have corrupted the body state estimate in the PPC, with the result that the body posture is unknown to the system, and movements cannot be corrected based on this estimated body posture. Similar mechanisms may underlie the motor planning deficits that are apparent in some forms of apraxia (Heilman et al. 1986; Halsband et al. 2001). Interestingly, apraxic patients also have difficulty in comparing visual and proprioceptive information during the generation of movement (Sirigu et al. 1999).

Estimation of Goal State in EBA

Activity in the EBA was specifically increased when subject's body posture was incongruent with the goal posture of the planned action. Although EBA was initially coined as a purely "visual" area that is involved in the perception of body parts (Downing et al. 2001; Urgesi et al. 2004), later studies suggest that EBA also has a role during planning of voluntary manual actions (Astafiev et al. 2004; Kuhn et al. 2011). According to the ideomotor theory, actions are accessed via representations of the sensory effects they evoke (Hommel et al. 2001). In this framework, the role of the EBA may to provide a predicted goal state of one's hand, on the basis of which the action plan is elaborated (Kuhn et al. 2011). The activity increase in EBA was not correlated with RT increases when subject's body posture was incongruent with the action's goal posture. While the interpretation of null findings is generally difficult, one possibility is that this stems from the fact that the EBA is only providing an initial estimate of the goal state, which constitutes the input to a motor simulation carried out in the IPS. The delay in onset of this motor simulation may be what underlies the RT increase. Indeed, there were consistent correlations between motor planning time and neural activity in the latter area (Figs 5C and 6C).

The notion that EBA provides a visual estimate of the hand's goal state for action planning is also supported by neuropsychological studies that observed impairments in the elaboration of action plans in visual agnosia patients with lesions in lateral occipital areas and occipitoparietal and occipitotemporal regions (Dijkerman et al. 2009). Despite being able to grasp and move objects according to instructions, these patients showed abnormal grip behavior in trials where start and goal postures differed, and an action plan had to be elaborated that required computing a goal posture. We suggest that EBA may therefore, in the context of action planning, represent the goal posture of a planned action. Such a sensory representation of the desired goal state will need to be held online for longer when the planning process is slowed down by the incongruence of one's own posture with the goal posture (as is evident from the behavioral results). Importantly, the goal representation in EBA is visual in nature and is not dynamically updated during the movement (unlike the body posture representation in IPS).

Conclusion

We have shown a facilitation of action planning when one's physical body posture is congruent with the action's goal posture. This facilitation is visible in behavior and in neural structures that contain body representations: the IPS and EBA. Specifically, our neuroimaging data suggests that IPS maintains an internal state of one's own body posture during the planned action, while EBA contains a representation of the action goal posture. Together, this study elucidates how action plans are elaborated in terms of their distal goals and how planning of actions interacts with one's own body, emphasizing the embodied nature of motor planning.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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