Posture influences estimates of body representations during motor planning: an fMRI study

Marius Zimmermann[1]
Supervisors: Ruud GJ Meulenbroek[2], Floris P de Lange[1]

[1]Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands
[2]Donders Centre for Cognition, Nijmegen, The Netherlands

It is still an open issue how we generate motor plans to attain our goals. Several studies suggest that motor planning is a hierarchical process that is organized around the action outcome or goal. Moreover, action selection depends on the current state of one's own body. In this study we investigated how one's own body posture interacts with planning of goal-directed actions. Participants engaged in an action planning task while we manipulated their arm posture. Behavioral results indicate that motor planning is facilitated when one's own body state is congruent with the goal posture, rather than begin posture, of the planned movement. fMRI results showed that two regions that are involved in body representation, the intraparietal sulcus (IPS) and the extrastriate body area (EBA), showed an interaction between body posture and action planning. There was more activity in IPS when the body posture was overall incongruent with the action plan, whereas EBA was specifically more active when the body posture was incongruent with the goal posture of the planned action. This suggests that IPS maintains an internal state of both one's own body posture and the body posture used in a planned action, while EBA contains a representation of the action's goal posture. 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.

Keywords: motor simulation, parietal, premotor, movement representation, motor imagery

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Corresponding author: Marius Zimmermann, E-mail: m.zimmermann@donders.ru.nl

1. Introduction

When we have a goal (such as drinking a cup of tea), the central nervous system (CNS) has to find a solution to achieve this goal, using a set of motor commands (e.g. reaching for and grasping of a cup, then moving it to the mouth). However, our body has abundant degrees of freedom (Bernstein, 1967), which enables us to achieve goals using a wide range of actions, but at the same time poses the problem that there is no unique solution. Selecting the optimal solution is a fundamental decision process that depends on both the state of our body and the context at hand (Kording and Wolpert, 2006).

It is generally assumed that the CNS selects actions that are optimal in respect to criteria like smoothness (Flash and Hogan, 1985) or energy costs (Alexander, 1997) of the movement. Crucially, motor planning appears to be organized around distal goals (Grafton and Hamilton, 2007). In line, Rosenbaum and colleagues suggest that, often, rather than optimized movement trajectories, optimized goal-states have highest priority in planning of goal-directed actions. Depending on the action's goal different criteria are optimized, for example precision in dancing or impact in boxing. Often it seems to be the comfort of end-postures that is maximized, at the cost of comfort of intermediate postures, which is known as the end-state comfort effect (Rosenbaum et al., 1992; 1995; 2001; 2009). For example, when a waiter wants to fill a glass that stands upside down on a table, he grasps the glass in an awkward way (thumb down) to turn it around, so he can hold it in a comfortable way (thumb up) during filling. But the suggestion that end-state comfort is optimized has been doubted by Herbort and Butz (2010), who suggest that, rather than optimizing the orientation of the goal state of an action, we make use of heuristic grip orientations when grasping objects for rotations (e.g. use a supine grip for counter clockwise rotations, and a prone grip for clockwise rotations).

Neurally, support for motor planning in terms of goal states is provided by Graziano et al. (2002). They applied microstimulation at behaviorally relevant timescales to neurons in premotor cortex of monkeys, which resulted in movements towards neuron specific postures, independent of the initial body posture. These neurons therefore represent goal states of the body rather than specific movements or muscles.

Behaviorally it has been shown that the ease with which motor plans are generated is affected by changing one's body posture (Sirigu and Duhamel, 2001). Therefore, planning may be facilitated when one's body state is congruent with an action's goal state. The CNS estimates body states using forward models (Grush, 2004) that are maintained in the intraparietal sulcus (IPS) of the parietal cortex (Wolpert et al., 1998; Wolpert and Ghahramani, 2000). Additionally, the extrastriate body area (EBA, Downing et al., 2001) seems to be involved in representing end-states of manual actions during motor preparation (Astafiev et al., 2004; Kuhn et al., in press). Previous research (de Lange et al., 2006) already reported modulation of activity in IPS by body posture during motor simulation, and EBA activation seems to be modulated by the availability of proprioceptive information in Parkinson's disease patients (Helmich et al., 2007).

Here, we want to investigate how one's own body posture interacts with motor planning. For this, participants engaged in a planning task involving grasping and placing of an object, while we manipulated their arm posture. In neural terms, we expect modulation of activity in IPS and EBA by body posture in motor planning. Behaviorally, we expect planning to be facilitated when one's body posture is congruent with the goal-posture of the planned movement, in case start- and goal-posture of the planned action differ from each other, such as when the waiter turns the glass right-side up. This would support the notion that action planning is organized around goals and, at a lower level, in terms of goal states of the body. On the other hand, facilitation by congruence between one's physical hand posture and an action's start posture could be expected from a heuristic approach to action selection, where the goal state is less important to plan an action.

2. Methods

2.1 Participants

Twenty participants (13 female) with an average age of 23.1±1.6 (mean±SD) years participated after giving informed consent according to institutional guidelines (CMO region Arnhem-Nijmegen, The Netherlands) for payment of 10 euros/hour or course credit. All of them were right handed and had normal or corrected-to-normal vision. One of the participants was excluded from the analysis of behavioral data because responses were not correctly recorded. Two others were excluded because of ideosyncratic performance on both motor execution and planning tasks (grip preference >3 SD from mean grip preference).

2.2 Task

Participants engaged in a motor execution (ME) and motor planning (MP) task subsequently. We acquired functional magnetic resonance imaging (fMRI) data during the MP task only.

2.2.1 Motor execution (ME) task

Three cradles were positioned on a table next to each other at 5 cm distance between adjacent cradles. We instructed participants to grasp a bar (length: 25cm, diameter: 2.5cm) that was lying on the middle cradle using a full hand (power) grip and place it according to instructions we presented on a screen. One half end of the bar was painted black, the other half white. Instructed actions always involved a direction (i.e. whether to place the bar on the left or right cradle), and final bar-orientation (Figure 1).

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 degrees rotation. We also included trials in which the bar had to be placed vertically (requiring a 90 degrees rotation), to allow for comparison with earlier studies (Rosenbaum et al., 1992). Each trial started with the bar lying on the middle cradle, with the white end either to the left or right side. We instructed participants to rest their hand on the table prior to every trial with the palm facing either up or down, changing after every eighth trial. During the task, we tracked participants' hand position using a three-dimensional motion tracking device (Polhemus Liberty, using 2 sensors at the left and right edge of the wrist of the right arm, sampling at 240 Hz). We established movement times and grip choice from these recordings offline.

2.2.2 Motor planning (MP) task

Participants engaged in a motor planning task while whole-brain activity recordings were made using fMRI. During the MP task, participants saw a picture of a bar on the middle one of three cradles, representing the start configuration of trials in the ME task. We used the same instructions to signal the desired goal orientation and position of the bar (Figure 2), but in the MP 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 one of two buttons with their index and middle finger of their left hand. We established reaction times and grip choice from these responses.

During the MP task, we manipulated participants' right arm posture: participants had to keep their right hand in a palm up or palm down orientation for blocks of eight trials. Since no overt movements had to be performed, hand posture did not change during a trial. This resulted in different patterns of congruency between a subject's own hand posture and the hand posture(s) during planned hand movements. During trials requiring no bar rotation but only bar translation (NO ROTATION trials), participants' posture could either be 'overall congruent' or 'overall incongruent' with the planned action (because the start- and goal-posture are the same for these actions, see Figure 2). During trials requiring a bar rotation (ROTATION trials),

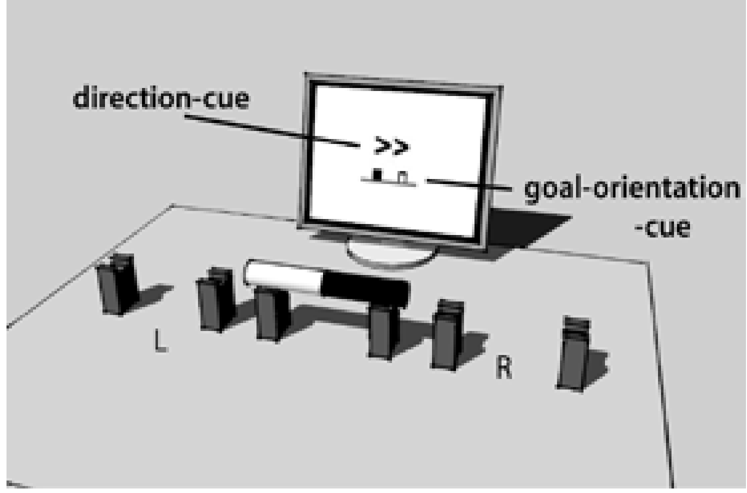

Fig.1 Motor execution (ME) task. A cylindrical bar is placed on the centre cradle. Trial instructions are provided on the screen. In the example, the instructions require the subject to place the bar on the right cradle (R), as indicated by the direction cue, and with the black end to the left, as indicated by the goal-orientation cue. In this example a rotation of the bar is required.

participants' posture could either be in a 'start-posture congruent' posture or 'goal-posture congruent' posture with the planned action (because the action involves a rotation, start- and goal-posture are necessarily opposite). During trials requiring 90 degrees 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). Conditions are illustrated in Figure 2.

2.3 Experimental procedure

Upon arrival in the lab, we introduced participants to the kinematics lab where we administered the ME task. They were made comfortable with the recording device, we attached sensors required for motion tracking to their wrist, and introduced them to the task. After a short (~5 trials) training participants were able to perform the ME task. They completed 96 trials (32 rotation, 32 no rotation, and 32 vertical trials) in about 20 minutes.

Next, we brought participants to the MRI lab, where they were checked for MR compatibility and introduced to the MP task. They performed 15 practice trials outside the scanner, followed by 40 practice trials inside the scanner (during T1 scanning). The MP task itself consisted of 320 trials (120 no rotation, 120 rotation, 80 vertical), and lasted 45 minutes. We divided the task in two sessions of 25 and 20 minutes. After the experiment participants were debriefed and rewarded. Total lab time of participants, including all preparation phases, was about two hours.

2.4 Behavioral data acquisition

During ME, we measured hand position over time using two motion tracking sensors (Polhemus Liberty, sampling frequency: 240 Hz) attached to both sides of participants wrists and saved the data for offline processing and analysis. For preprocessing, we sequenced hand trajectories into different parts on a trial-by-trial basis. The first part was defined as the hand's movement from the resting position until grasping of the bar; the second part as the object transportation until placing at the target; and the remaining part was defined as the return phase, which is of no further interest. For sequencing we combined a predefined target region with a minimum-speed approach. Sequences were divided at the moment when (a) the hand was close to the bar (within box range of 10x5x5 (width, depth, height) cm centered on the cradles), and (b) the hand's velocity was at its lowest within that area. For each trial/movement we retrieved three time points: when a subject starts moving, when he grasps the bar, and finally, when he places it. Additionally, we retrieved hand orientation at the moments of grasping and placing. We based error detection on deviant hand orientation compared to the trial instructions, and removed those trials (on average, 4.2% of the trials were removed by this procedure).

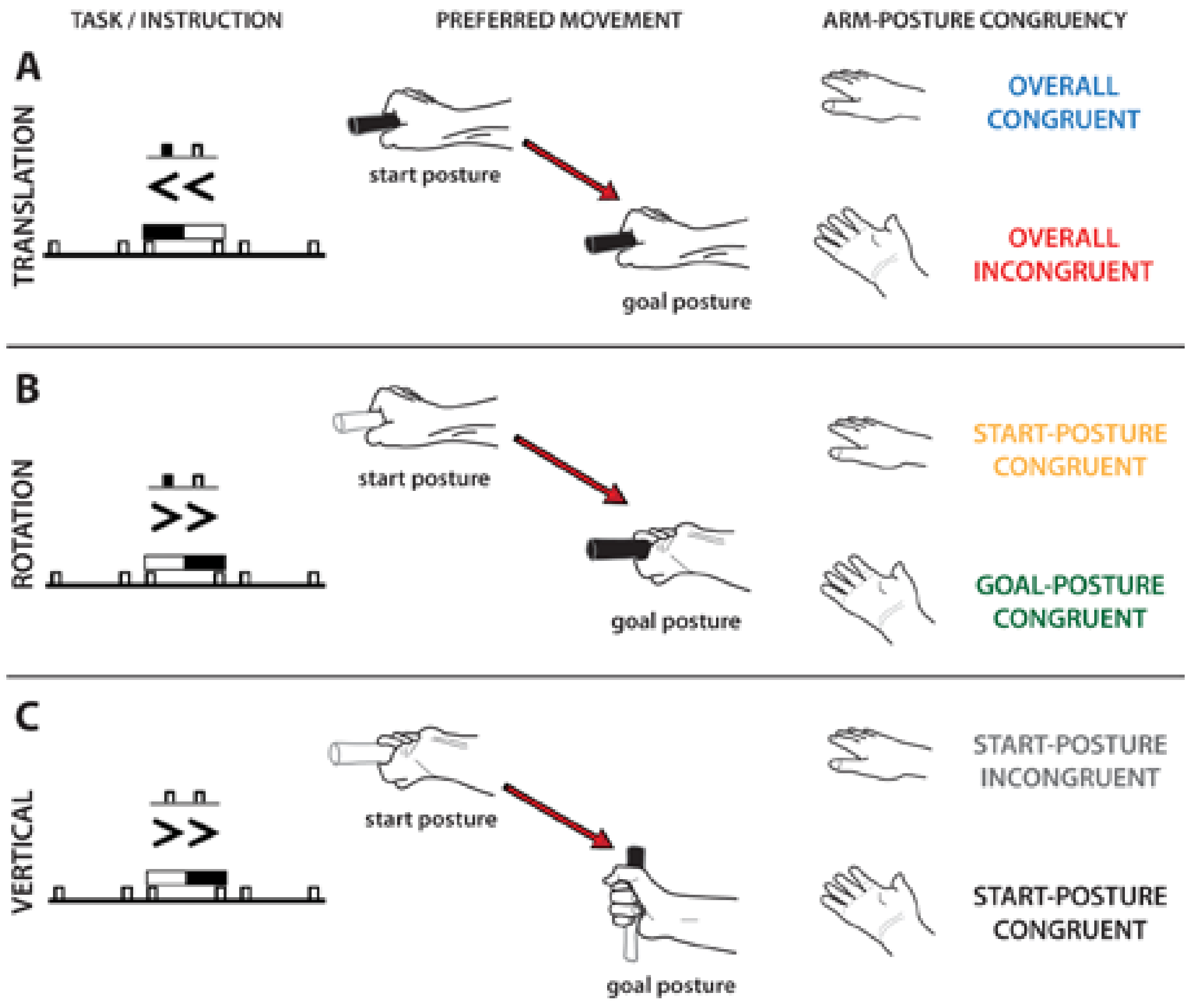

Fig. 2 Motor planning (MP) task. Stimuli and conditions of motor planning (MP) task with translation **(A)**, rotation **(B)** and vertical **(C)** trials. Left column shows example stimuli (compare Figure 1). Middle column shows preferred start- and goal-posture during the movement. Right column shows 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.

During MP, we used button box responses to establish hand orientation of planned grasping (by combining the response with the instruction about initial bar orientation per trial), and response latencies as movement planning times. Trials with reaction times two standard deviations above a participant's condition mean were removed from analysis (on average, 8.41% of the trials were removed by this procedure).

2.5 Behavioral data analysis

We used Matlab 7.9 for behavioral analyses. First, we compared grip preference and movement/planning times between tasks to ensure their common grounding on motor control, using a correlation approach. For each condition (target direction, initial orientation, final orientation, and initial posture) we computed average movement and planning times as well as average grip preferences.

We defined grip preference as the ratio underhand grip/trials per condition, leading to values between 0 (always overhand) and 1 (always underhand). We defined planning times as the time required to give a response and movement times as the time to place the bar onto the target cradle. In a further step we computed group means for all conditions over both tasks, which we tested for correlation.

Then, we analyzed reaction times from the MP task for action complexity- and posture-effects. As a measure of the action complexity effect we used the reaction time difference between easy (i.e. NO ROTATION) and difficult (i.e. ROTATION) trials. Posture effects were analyzed for each trial type apart: in NO ROTATION trials a posture effect was defined as the difference in reaction time with an overall congruent and overall incongruent posture; in ROTATION trials posture effect was defined as the reaction time difference between trials where participants own posture reflects the start posture and trials where the own posture reflects the goal posture of the planned movement; in VERTICAL trials posture effect was defined as the reaction time difference between trials where participants own posture does reflect the start posture and trials where it does not.

2.6 Image data acquisition

We used a 1.5 T Avanto MR-scanner (Siemens, Erlangen, Germany) to acquire whole-brain T2*-weighted gradient-echo echo-planar images (TR=2140ms, TE=40 ms 3.5x3.5x3.0 mm voxels, inter-slice gap = 0.5 mm). We used a 32-channel head coil for signal reception. Per participant, a total of about 1400 volumes were collected. The first 5 volumes of each scan were discarded to allow for T1 equilibration effects.

2.7 Imaging data analysis

Imaging data were analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London, UK). For preprocessing, all images were realigned spatially to the first volume, and the signal in each slice was realigned temporally to the first slice using a sinc interpolation.

Resliced volumes were then normalized to a standard EPI template based on the MNI reference brain in Talairach space. The normalized images were smoothed with an 8-mm FWHM isotropic Gaussian kernel. Treating the volumes as a time series, the data were high-pass filtered to 1/128 Hz. Smoothed images were scaled to a grand mean of 100 over all voxels and scans within a session.

Three times two event types were defined: (1) NO ROTATION trials, which were further divided into those with (1a) overall congruent, and (1b) overall incongruent posture; (2) ROTATION trials, which were further divided into those with (2a) start posture congruent, and (2b) goal posture congruent posture; and (3) VERTICAL ending trials, which were further divided into those with (3a) congruent start posture and (3b) incongruent start posture. Note that for the latter trial type, the own posture and planned end posture are always incongruent.

Each analysis was performed in a two-stage procedure. In the first stage, the BOLD response for each event type was modeled with the canonical HRF and its temporal derivative. These functions were convolved with an event train of short boxcar functions at each stimulus onset, and used to create covariates in a GLM. The length of the Boxcar functions was defined as a participant's average reaction time. Parameter estimates for each covariate were calculated from the least-mean-squares fit of the model to the time series. Images of the parameter estimates for the canonical and derivative covariates were created by subject-specific contrasts (collapsing across sessions within subjects). These "summary statistic" images comprised the data for a second stage of repeated-measures analyses, treating subjects as a random variable. Pairwise one-tailed contrasts on the canonical parameter images allowed t-tests on differences in the magnitude of event-related responses. We included for each participant the effect size as covariate in the analysis of magnitude differences.

Canonical SPMs were thresholded at $p < .001$. Additionally, analysis was restricted to clusters that were comprised of at least 10 voxels. Regions of interest (ROI) were selected based on previous research. For SPL [-22 -60 58] we used coordinates from de Lange et al. (2006), for EBA [-49 -72 -2] we used coordinates from Downing et al. (2001). Statistics were done on small volume corrected regions of 10 mm spheres around ROIs. Maxima of identified regions were localized as good as possible to the system of Talairach and Tournoux (Talairach and Tournoux, 1988).

3. Results

3.1 Behavioral Results

3.1.1 Motor execution

We obtained movement time (MT) measures and observed grip preference during the motor execution task. MT was larger for trials that required a rotation of the bar (ROTATION trials) than trials that did not (NO ROTATION trials, see Fig 2 for examples) (difference=418 ms: t=7.299, p<.001). Based on comfort ratings for various postures taken from Rosenbaum (1992) we predicted whether for a particular action sequence in our task participants would prefer an initial over- or underhand grip. Observed preferences during movement execution strongly correlated with predicted grip preferences (r=.941, p<.001), in line with models of end-state comfort.

3.1.2 Motor planning

We collected reaction time (RT) measures and indicated grip preference during the motor planning task. In good correspondence with the motor execution task, participants were slower in ROTATION trials than NO ROTATION trials (difference: 383ms, F(1,16)=41.177, p<.001), and when comparing RTs for different action plans with MTs for corresponding action plans, there was a tight correlation between these two (r=.86, p<.001, Figure 3a). Also, indicated grip preference correlated strongly with predicted grip preferences (r=.857, p<.001), and with grip preferences obtained from the ME task (r=.97, p<.001, Figure 3b). Together, these data indicate that the duration and outcome of cognitive processes during the motor planning task are highly similar to those observed during actual motor execution.

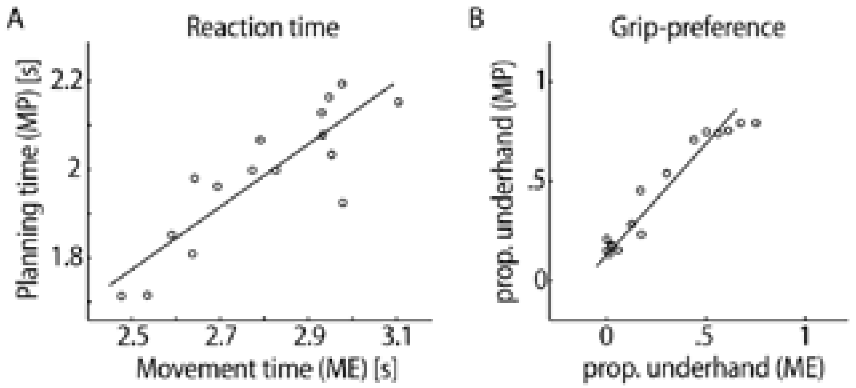

Fig. 3 Comparison of behavioral performance during ME and MP task. Average movement times **(A)**, in seconds and grip preference **(B)** proportion underhand grips) during ME for all possible movements are highly similar to average reaction times and preference during MP for corresponding movement types.

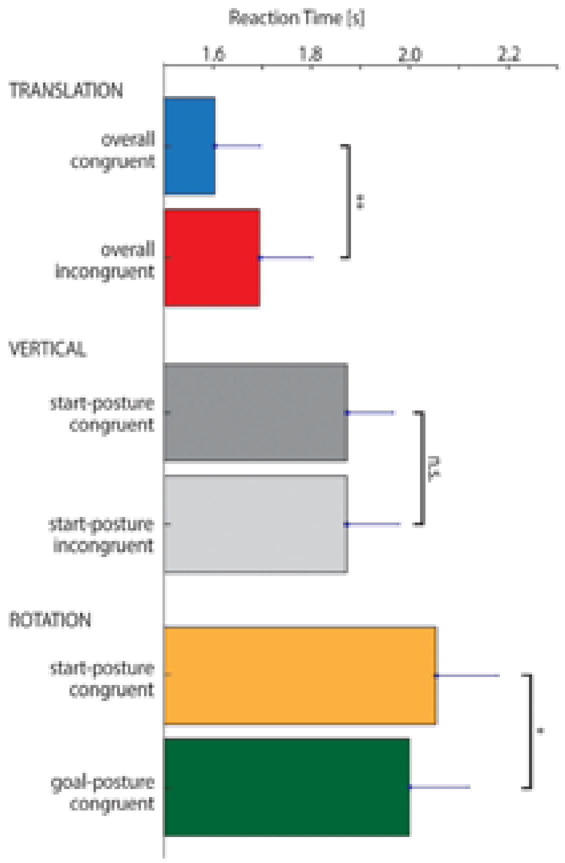

Fig. 4 Behavioral performance during MP task. Plotted are averages of planning times for different movement types (translation, vertical, rotation) as well as effects of posture congruency on each movement type. See Figure 2 for detailed description and color coding of conditions.

3.1.3 Effect of hand posture

We next assessed the effect of hand posture on RT during the motor planning task. During NO ROTATION trials, participants' posture could either be 'overall congruent' or 'overall incongruent' with the planned action (because the start- and goal-posture are the same for these actions, see Figure 2). Participants were faster with their hand in an 'overall congruent' posture than in an 'overall incongruent' posture (difference=93 ms: F(1,16)=9.916, p=.006). During ROTATION trials, participants' posture could either be in a 'start-posture congruent' posture or 'goal-posture congruent' posture with the planned action (because the action involves a rotation, start- and goal-posture are necessarily opposite). Here, participants were faster when their hand was in a 'goal-posture congruent' compared to a 'start-posture congruent' posture (difference=54 ms: F(1,16)=4.713, p=.045). During VERTICAL ending trials posture manipulation had no effect on RTs (F(1,16)=0.002, n.s.; p=.962), that is, they were equally fast regardless of whether their own posture was congruent or incongruent to the start-posture of the planned movement.

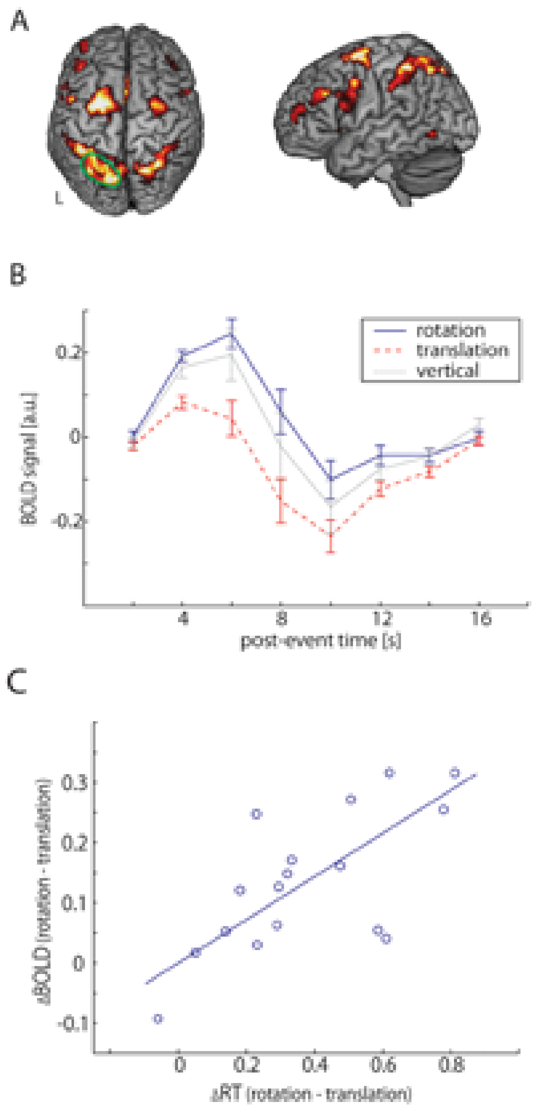

Fig. 5 Neural activity modulated by complexity of movement plan. **(A)** Brain rendering showing areas that were significantly more activated as a function of movement complexity during the MP task (rotation > translation, thresholded at T > 4 for display purposes). **(B)** Event-related response of 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.

3.2 Neural Activity

3.2.1 Movement complexity

When comparing ROTATION with NO ROTATION trials, we observed increased activity in a network spanning superior parietal, dorsal precentral and inferior frontal cortex (Fig 5A-B). A correlation analysis showed that there was a tight link

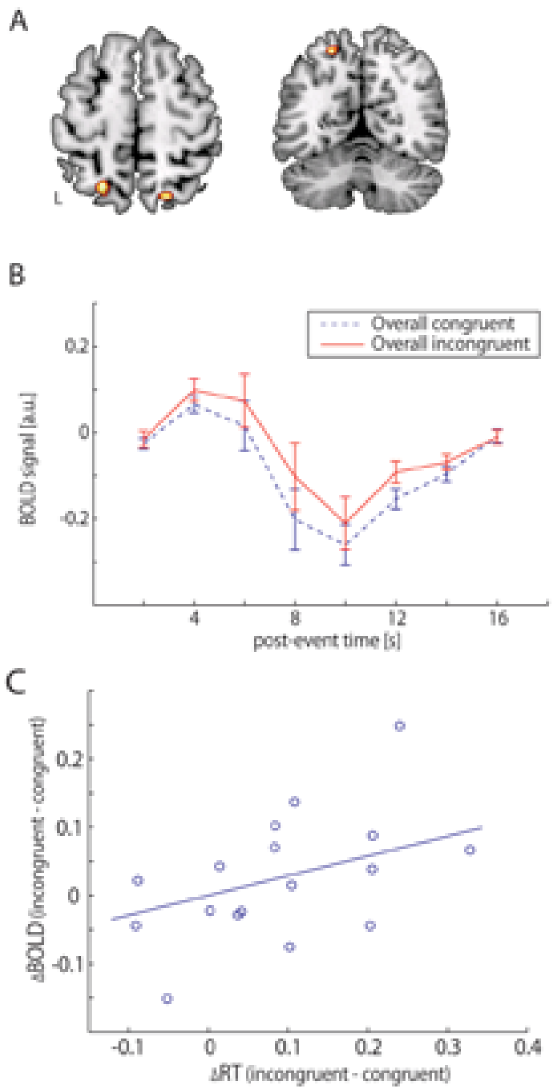

Fig. 6 Neural activity modulated by overall body posture congruency. **(A)** Anatomical localization of areas that were more active when body posture was overall incongruent with the movement plan during the MP task (thresholded at T > 2 for display purposes). **(B)** Event-related response of left IPS, 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.

between inter-subject variability in RT differences between ROTATION and NO ROTATION trials on the one hand and neural activity difference s between these conditions on the other hand in the left superior parietal lobe (r=.682, p<.01). A complete list of activated brain regions can be found in the supplementary materials.

3.2.2 Effect of hand posture

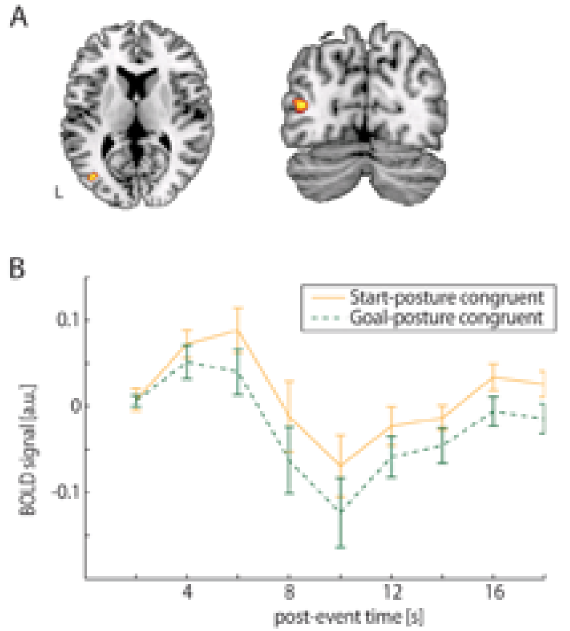

Fig. 7 Neural activity modulated by goal-posture congruency. **(A)** Anatomical localization of areas that were more active when body posture was incongruent with the goal posture of the movement plan during the MP task (thresholded at T > 2 for display purposes). **(B)** Event-related response of left EBA, plotted for different levels of body posture congruency. For details on conditions and color coding, see Figure 2.

During NO ROTATION trials, we observed increased neural activity in the left and right SPL when subject's hand posture was overall incongruent with the planned action (Figure 6A-B). Moreover, inter-individual differences in BOLD activity between congruent and incongruent posture conditions correlated with differences in reaction times between postures (Figure 6C: r=.521, p<.05).

During ROTATION trials, neural activity increased when participants adopted a start-posture congruent hand posture (compared to goal-posture congruent hand posture) in the left middle occipital gyrus, falling close to the putative extrastriate body area (EBA: euclidean distance = 7 mm; Downing et al., 2001).

Manipulation of hand posture had no effect on VERTICAL ending trials where participants were instructed to place the bar vertically between a cradle pair, that is, with the own hand posture congruent or incongruent to the start-posture of the movement alone (while always incongruent with the goal-posture). For a summary of all posture effects see Table 1.

4. Discussion

Table 1. Posture congruency effects during the motor planning task. 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.

Contrast	Anatomical region	MNI coordinates			Cluster size	*t*-value
		x	y	z		
Incongruent > congruent overall posture (translation trials)	**Intraparietal sulcus**	-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

This study investigated how one's own body posture interacts with the planning of goal-directed actions. Behavioral results supported the hypothesis that motor planning is facilitated when one's body state is congruent with the goal-posture of the planned movement. In neural terms, two regions were modulated by body posture: the superior parietal lobe (SPL) and the extrastriate body area (EBA). SPL was more active when the body posture was different from the posture used in a motor plan for translation of an object than when postures were the same. EBA was more active when the body posture was the same as the start-posture used in a motor plan for rotating an object compared to when it was the same as the goal-posture of the same motor plan. 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. This is in line with models that suppose that movement planning is predicated on the specification of goal postures (Rosenbaum et al., 2001; Graziano et al, 2002).

4.1 Behavioral results - Importance of end-posture in movement planning

When participants decided how to grasp the bar, they predominantly selected the option that had a comfortable end-posture, which suggests that motor planning determines the solution to the selection problem on the basis of the end-state of an action. This is further supported by the observation that planning of movements is facilitated when proprioceptive information about one's body state is congruent with the movement's goal-state. Thereby, our behavioral results support Rosenbaum's theory, that movement planning is organized around goal postures.

4.2 Parietal and premotor cortex are modulated by movement complexity

The motor planning task activated a fronto-parietal network comprising the superior parietal, dorsal precentral and inferior frontal cortex. Activity within this network increased with increasing complexity of the movement plan, from a simple translation to combined translation and rotation movements. The involvement of superior parietal and dorsal precentral cortex during the elaboration of motor plans is in line with previous studies of movement planning in humans (Beurze et al., 2007) and monkeys (Kalaska et al., 1997; Scott et al., 1997).

4.3 Body posture interacts with motor planning

There were two regions whose activity was modulated by participant's body posture during the movement planning task: SPL and EBA. Interestingly, both of these have been suggested to contain a body representation (SPL: Wolpert et al., 1998; Ehrsson et al., 2000; EBA: Downing et al., 2001; Astafiev et al., 2004; Saxe et al., 2006; Kuhn et al., in press). In our study, SPL showed increased activity during planning of simple translation movements when one's arm posture was different from the posture used in the motor plan. EBA showed increased activity during planning of more complex rotation movements when one's arm posture was different from the goal posture. In the following section, we will discuss potential functions of both areas during the generation of a motor plan.

4.3 Body state estimation in posterior parietal cortex

The parietal cortex integrates sensory information from multiple modalities with motor plan information from efference copies (Andersen et al., 1997). These sources of information can be used to generate an estimate of a body state, in order to achieve an optimal representation of the current body state and predict future states (Wolpert and Ghahramani, 2000; Grush, 2004). Our finding of increased activation in the parietal cortex when there was larger incongruence between one's arm posture and the planned arm posture in translation movements is supportive of this idea. The enhanced activation can be related to the larger computational load necessary to merge the proprioceptive body-related information with the motor plan. This is compatible with earlier studies on mental simulation of reaching (de Lange et al., 2006) and grasping movements (Grezes et al., 2003; Vargas et al., 2004).

Surprisingly, SPL was not modulated by body posture when participants planned complex rotation movements. During generation of these motor plans body posture was congruent to either the start- or goal-posture of the planned movement. Absence of activation differences may however be related to the fact that congruent and incongruent phases cancel out each other in these motor plans. That is, if body posture is congruent with the start-posture of the planned movement then we expect low activity when estimating early parts of the motor plan, but high activity when estimating later parts of the motor plan, and vice versa when body posture is congruent with the goal-posture. The temporal difference may be too small to be detected in the slow BOLD signal. Clarification could be given by neuroimaging techniques with high temporal resolution like MEG or EEG.

4.4 Goal-state estimation in EBA

Besides SPL, EBA was modulated by body posture in complex trials that involved rotation of the bar. Originally, EBA has been assumed to be a pure visual area involved in the perception of body parts (Downing et al., 2001). However, later studies showed that EBA is also activated during planning of voluntary manual actions (Kuhn et al., in press), and is involved in representing one's body by combining information from multiple modalities (Astafiev et al., 2004). Here we observed that EBA is more active during movement planning when one's body posture is incongruent with the goal-posture of a motor plan. This suggests that EBA may contain a visual or multimodal representation of an action's goal-state when a motor plan is generated. This may make EBA a candidate region involved in the selection of an appropriate goal-posture, which results in the earlier mentioned end-state comfort effect. Such a representation of the goal-state may be evaluated in terms of comfort and other aspects.

There are two possibilities how EBA may be involved in motor planning. One possibility is that EBA is involved early during the generation of a motor plan, which is motivated by Kuhn et al. (in press). In a given task, a visual representation of the desired goal-posture may be generated in EBA in visual terms. Subsequently, as assumed in ideomotor theory (Hommel et al., 2001), the visual representation may activate a motor plan that achieves the desired goal-state. Another possibility, motivated by Astafiev et al. (2004), is that a body representation in EBA is updated by efference copies of an earlier generated motor plan (that is, EBA is involved later on during motor planning). This updated body representation may then be evaluated, leading to for example movements that are finished with a comfortable body posture.

However, EBA was not modulated by body posture during the planning of simple translation actions. This lack of modulation may be the result of the fact that overall less computation was required for these simple actions. In a study by Helmich et al. (2007), EBA was increasingly activated with biomechanical complexity of a movement, particularly in Parkinson's disease patients, which may reflect increased reliance on a visual representation of one's body during planning. A study by Dijkerman et al. (2009) gives additional, indirect support for the idea that EBA is especially involved in planning of complex actions. They tested patients with lesions in lateral occipital areas and occipito-parietal and –temporal regions in a task that, even stronger than our task, predicts actions according to the end-state comfort effect. Despite being able to grasp and move objects according to instructions, patients showed abnormal grip behavior in more complex trials. EBA may therefore not be critical for planning, but recruited in order to improve grasping behavior.

4.5 Conscious report of grip orientation

A critical point in this study is that in normal behavior grip selection might be rather automatic and its outcome (such as the arm orientation during grasping) might not be consciously available to the actor. Here, we asked participants to indicate by button press how they would grasp a button, which might interfere with the processes in a way that is not controlled for by contrasting of conditions (i.e. subtraction method). The manipulated factor hand posture may influence the ease with which participants in our study can report their grip orientation. In particular, the adopted hand posture can be congruent or incongruent to the hand orientation inherent to the report participants have to give. For example, when in the initial bar configuration the black part is on the left end, and subjects use an overhand grip, they have to press the button assigned to black. The inherent orientation to grasp the bar such that one's thumb rests on the black end is an overhand (prone) grip orientation. If body posture does effect the ease with which a report is given, we should see facilitation when one's body posture is congruent to the begin state of the planned action. The results however showed the opposite pattern, meaning that it is highly unlikely that the observed goal state facilitation resulted from such interference. Furthermore, such an effect should especially be visible during the VERTICAL condition, where congruency was only manipulated between one's physical body posture and an action's start posture.

5. Conclusions

Behaviorally we observed facilitation of motor planning if one's body posture is congruent to the goal-state (but not its begin-state) of the planned movement. Neurally we observed that SPL and EBA are differentially modulated by one's own body posture during motor planning. From these results we conclude that the SPL maintains an internal representation of one's own body, while a visual representation of a movement's desired goal-state is generated in EBA. The former is probably used to inform motor plans about object properties (Davare et al., 2010), and the latter one may be used to improve our behavior in characteristics that are not directly linked to the success of actions.

From the behavioral results as well as activation differences in SPL and EBA we conclude that motor planning is organized around goal postures rather than discrete limb or joint movements. Moreover, we can conclude that one's body posture is relevant in the generation of motor plans, which emphasizes the embodied nature of motor planning.

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