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The influence of action possibility and end-state comfort on motor imagery of manual action sequences

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ABSTRACT

It has been proposed that the preparation of goal-direct actions involves internal movement simulation, or motor imagery. Evidence suggests that motor imagery is critically involved in the prediction of action consequences and contributes heavily to movement planning processes. The present study examined whether the sensitivity towards end-state comfort and the possibility/impossibility to perform an action sequence are considered during motor imagery. Participants performed a mental rotation task in which two images were simultaneously presented. The image on the left depicted the start posture of a right hand when grasping a bar, while the right image depicted the hand posture at the end of the action sequence. The right image displayed the bar in a vertical orientation with the hand in a comfortable (thumb-up) or in an uncomfortable (thumb-down) posture, while the bar in the left image was rotated in picture plane in steps of 45°. Crucially, the two images formed either a *physically possible* or *physically impossible to perform* action sequence. Results revealed strikingly different response time patterns for the two action sequence conditions. In general, response times increased almost monotonically with increasing angular disparity for the possible to perform action sequences. However, slight deviations from this monotonicity were apparent when the sequences contained an uncomfortable as opposed to a comfortable final posture. In contrast, for the impossible sequences, response times did not follow a typical mental rotation function, but instead were uniformly very slow. These findings suggest that both biomechanical constraints (i.e., end-state comfort) and the awareness of the possibility/impossibility to perform an action sequence are considered during motor imagery. We conclude that motor representations contain information about the spatiotemporal movement organization and the possibility of performing an action, which are crucially involved in anticipation and planning of action sequences.

1. Introduction

Object manipulations are, not surprisingly, influenced by a number of factors. How we grasp an object depends upon the physical properties of the object (Smeets & Brenner, 1999), the affordances that the object offers (Sartori, Straulino, Castiello, & Avenanti, 2011), the context in which the action is embedded (Borghi, Flumini, Natraj, & Wheaton, 2012), recently performed movements (Schütz, Weigelt, Odekerken, Klein-Soetebier, & Schack, 2011), and the intended action goal of the task (Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012).

In a pioneering study, Rosenbaum et al. (1990) had participants grasp a horizontally arranged wooden bar and place the left or right end of the bar into a target disk (hereafter referred to as the bar-transport task). The authors found that all participants selected initial grasps that would result in comfortable thumb-up postures at the end of the movement (i.e., end-state comfort). Thus, participants selected an initial overhand grip when the right end of the bar was to be placed to the target disk and an initial underhand grip when the left end of the bar was to be placed to the target disk.

This seminal article, as well as subsequent research, has provided strong evidence that premotor representations are used when selecting among different movement alternatives, and that object manipulation movements are planned with respect to future goal postures (Hughes, Seegelke, Spiegel et al., 2012; Rosenbaum,

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Meulenbroek, Vaughan, & Jansen, 2001; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992).

Consistent with this representational tenet, it has been proposed that the preparation of goal-direct actions involves an internal simulation of the to-be-performed movement (aka motor imagery; Jeannerod, 1994, 1995). Motor imagery involves similar (neural) mechanisms as those activated when planning and executing overt movements (Decety et al., 1994; Jeannerod, 2001; Johnson, 2000; Parsons et al., 1995; Pfurtschneller & Neuper, 1997; Roth et al., 1996), and thus, as actual motor performance, is strongly affected by the biomechanical constraints of the body.

For example, Johnson (2000) had participants reach out and grasp a dowel placed in different orientations (*actual* task performance) or verbally judge how they would grasp the dowel without executing the reach-to-grasp action (*mental* task performance). Results showed great similarity in grip selection between mental and actual task performance. Moreover, when asked to rate the awkwardness of the grip values were similar regardless of task performance condition. In addition, RTs increased as a function of the angular distance between participants' current hand orientation, and the orientation of the chosen posture were longer for more awkward grasp postures for both task performance conditions.

On a behavioral level, motor imagery has often been studied using a mental rotation paradigm in which the participant compares two pictures that depict objects in different orientations and decide whether the objects are identical or mirror images (Shepard & Metzler, 1971). When the stimuli consist of bodies or body parts, the time for imagined spatial transformation of the stimuli strongly depended on the direction of the orientation difference, such that more time was required when the body parts were presented in physically awkward orientations (Parsons, 1987).

A later study (Petit, Pegna, Mayer, & Hauert, 2003) assessed mental rotation when a hand attached to a forearm was depicted in anatomically possible and impossible positions. That study showed that while RTs increased monotonically in both conditions, the speed of mental rotation was considerably slower for stimuli that depicted the arm in impossible configurations.

In sum, these studies provide strong evidence that biomechanical constraints are considered during both actual motor performance and motor imagery. However, to the best of our knowledge, there is no evidence whether individuals are not only sensitive to anatomically possible and impossible body configurations, but also to the general possibility/impossibility to perform an action sequence.

Taken these concepts into consideration, we asked the question as to whether individuals would consider *both* future goal postures (i.e., end-state comfort) and the possibility/impossibility to perform an action sequence during motor imagery. In the present experiment, participants performed a mental rotation version of the bar-transport task (Fig. 1). The stimuli consisted of two side by side images and participants were instructed that these images displayed an action sequence and that the left picture represented the start of the sequence and the right the end of the sequence. Participants had to judge as quickly and accurately as possible whether the two images represent an action sequence that is *physically possible* or *physically impossible* to perform. In contrast to previous mental rotation studies that used anatomically possible and impossible body configurations as stimuli (e.g., Petit et al., 2003), in the present study each individual image depicted a biomechanically possible grasp posture, but the images in combination depicted either a physically possible or physically impossible to perform action sequence.

Based on previous literature it was hypothesized that RTs would be shorter for sequences in which the hand was displayed in a comfortable final posture compared to sequences depicting

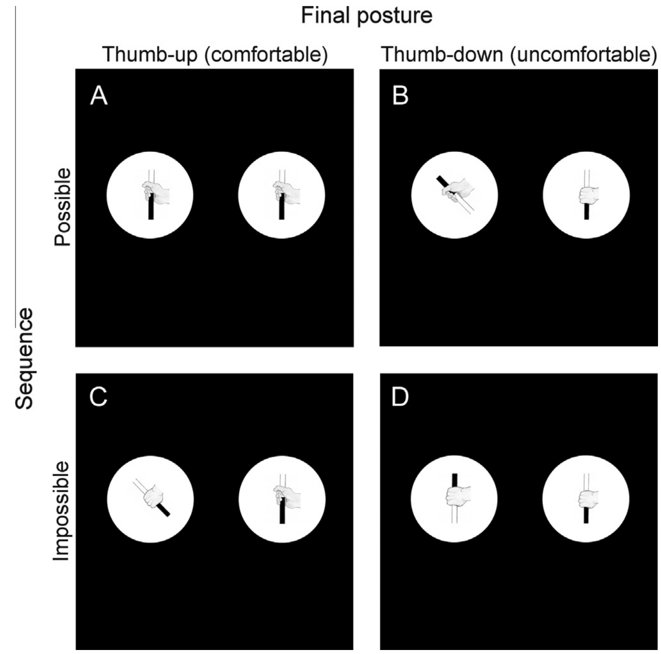

Fig. 1. Four exemplary stimuli used in the experiment depicting possible (top row) and impossible to perform sequences (bottom row) with a comfortable thumb-up (first column) and uncomfortable thumb-down final posture (second column). (A) 0° angular bar disparity, (B) 135° counterclockwise angular bar disparity, (C) 45° clockwise angular bar disparity and (D) 180° angular bar disparity.

the hand in an uncomfortable posture, and for possible compared to impossible sequences. Additionally, we expected RTs to increase with increasing angular distance. However, the speed of mental rotation should be slower for the impossible compared to the possible sequences and slower for sequences displaying the hand in a comfortable final posture compared to sequences depicting the hand in a comfortable posture.

2. Methods

2.1. Participants

40 individuals from Bielefeld University participated in exchange for 5€ or course credit. Data from one participant were excluded from analysis due to high amount (21.3%) of incorrect responses. The remaining participants (mean age = 24.92, SD = 3.96, 16 men, 23 women, 37 right-handed, 2 left-handed) had normal or corrected to normal vision and declared themselves as neurologically healthy. The experiment was conducted in accordance with local ethical guidelines and conformed to the declaration of Helsinki. Participants gave their informed written consent to participate in the study.

2.2. Apparatus and stimuli

Stimuli were presented on a 43 cm computer display (SyncMaster 943T, Samsung) and controlled via Presentation® (Neurobehavioral Systems). Participants responded by pressing either a left (A) or right (L) button on the key board with their index fingers. The assignment of response buttons was counterbalanced across participants.

Each stimulus consisted of two images (each 10 cm in diameter) that were presented simultaneously next to each other on a black background (see Fig. 1). Each image displayed a hand grasping a bar (one end painted white the other black) with the thumb pointing toward the black or the white end. The bar orientation on the left image was rotated in picture plane (0°, 45° clockwise, 45° counterclockwise, 90° clockwise, 90° counterclockwise, 135° clockwise, 135° counterclockwise, or 180°) with one of the two possible grasp postures (thumb toward black or white end). The image on the right displayed the bar always in a vertical position with the black end down and with either the hand in a comfortable thumb toward the white end or an uncomfortable thumb toward the black end posture.

2.3. Procedure

After filling out the informed consent form, participants were seated in front of the computer and the task was explained. At the start of each trial, a fixation cross was presented for 500 ms, and then after a random time interval (500–1500 ms) the stimulus appeared and remained until the response was carried out. Participants were instructed that the two images depict a manual action sequence with the left image representing the start of the sequence and the right image representing the end of the sequence. Thus, the task can be regarded as a "bar-transport-and-rotation task" in which a bar is grasped from a certain start position and orientation with a specific initial grasp posture (left picture) and transported and rotated to a certain end position and orientation in an specific final posture (right picture) without changing the grip throughout the transport. Thus, for half of the trials, the depicted final hand-bar constellation in the right picture could be achieved through rotation from the hand-bar constellation in the left picture (physically possible to perform trials; Fig. 1 upper panels) whereas this was not possible for the other half of the trial (physically impossible to perform trials; Fig. 1 lower panels). Participants were asked to judge as quickly and accurately as possible whether the two images represent an action sequence that is *physically possible* or *physically impossible* to perform. In the case of an incorrect response, the word "Fehler" (German for "wrong") was displayed, thus providing the participants with immediate feedback. RTs were calculated as the time period (in ms) between stimulus onset and button press.

Participants performed 32 practice trials prior to the experimental test blocks to familiarize themselves with the task, where each condition was presented once in a randomized order. Participants then took a 2 min rest break, after which the experiment commenced. The experiment consisted of 320 test trials that were divided into two test blocks. Participants took a 2 min rest break between test blocks. Within each block, each possible combination of angular bar orientations of the left image (0°, 45° clockwise, 45° counterclockwise, 90° clockwise, 90° counterclockwise, 135° clockwise, 135° counterclockwise, or 180°), end posture of the final image (comfortable thumb-up, uncomfortable thumb-down), and sequence (possible, not possible) was presented five times in a randomized order. The entire experimental session lasted approximately 30 min.

2.4. Data analysis

Responses with RTs more than three standard deviations from the mean on a condition and participant basis (outliers, 0.0% of the data), as well as RTs for incorrect responses (4.9%) were excluded from the RT analysis.

RTs from correct trials and error rates (in %) were analyzed using 2 Sequence (possible, impossible) × 2 Final Posture (comfortable thumb-up, uncomfortable thumb-down) × 8 Bar Angular Disparity (0°, 45° clockwise, 45° counterclockwise, 90° clockwise, 90° counterclockwise, 135° clockwise, 135° counterclockwise, or 180°) repeated measures analyses of variance (RM ANOVAs).

In addition, we calculated mental rotation rates (in ms/°) for each combination of the factors Sequence and Final Posture by fitting regression lines to the RT data across the bar orientation angles (0–180°). The rates were then analyzed using a 2 Sequence (possible, impossible) × 2 Final Posture (comfortable thumb-up, uncomfortable thumb-down) RM ANOVA with Sequence Execution (possible, impossible) and Final Posture (comfortable thumb-up, uncomfortable thumb-down) as within-subject factors.[1]

3. Results

In a pre-analysis, we calculated Pearson's correlations between participants' RTs on correct responses and accuracy (percentage of correct responses). RTs were not correlated with accuracy ($r = 0.057$, $p = 0.730$) demonstrating the absence of a speed-accuracy trade-off in participants' performance.

3.1. RT

Analysis revealed a main effect of Sequence, $F(1,38) = 78.16$, $p < 0.001$, with longer RTs for stimuli depicting an impossible sequence (1623 ms) compared to stimuli depicting a possible sequence (1446 ms). The main effect of Bar Angular Disparity [$F(7,266) = 18.09$, $p < 0.001$] and the Sequence × Bar Angular Disparity interaction [$F(7,266) = 39.71$, $p < 0.001$] were also significant. Importantly, the three-way interaction also reached significance, $F(7,266) = 2.91$, $p = 0.046$ (see Fig. 2). For the possible sequences, RTs typically increased with angular disparity. In addition, post hoc pair wise comparisons (Bonferroni corrected) indicated that RTs were significantly longer for possible sequences with an uncomfortable final posture than for possible sequences with a comfortable final posture at 90° cw and 135° ccw angular disparities (both $p < 0.05$; Fig. 2A). In contrast, for the impossible sequences, RTs were relatively high, did not increase with angular disparity, and were similar regardless of final posture (all $p > 0.2$; Fig. 2B).

3.2. Error rate

Analysis revealed a significant main effect of Bar Angular Disparity [$F(7,266) = 2.97$, $p = 0.015$] and a significant Sequence × Bar Angular Disparity interaction, $F(7,266) = 8.32$, $p < 0.001$. Post hoc pair wise comparisons (Bonferroni corrected) indicated that the error rate increased with increasing angular disparity for the possible sequences whereas for the impossible sequences the error rate was similar regardless of angular disparity (all $p > 0.1$; Table 1).

3.3. Mental rotation rate

The main effect of Sequence [$F(1,38) = 78.19$, $p < 0.001$] and the Sequence × Final Posture interaction [$F(1,38) = 4.50$, $p = 0.041$] were significant. As shown in Table 2, for the impossible sequences mental rotation slopes were negative and similar regardless of final posture ($p = 0.321$). In contrast, for the possible sequences, slopes were positive and marginally more shallow for comfortable than for uncomfortable final postures ($p = 0.068$).

[1] Given that our stimuli depicted grasp postures of the right hand only, preliminary analyses were conducted to test whether RTs and error rates were influenced by response button assignment (left hand "physically possible", right hand "physically impossible" vs. left hand "physically impossible", right hand "physically possible"). Analyses yielded negative results regarding the factor "Response button assignment", indicating that it did not influence the pattern of results in the present task.

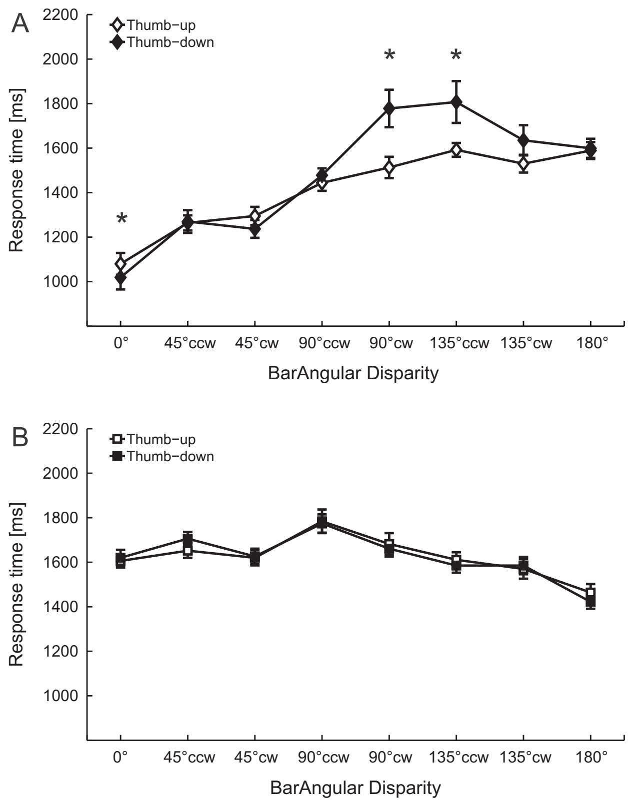

Fig. 2. Mean response times (in ms) as a function of bar angular disparity and final posture for the possible (panel A) and impossible (panel B) sequences. Asterisks indicate significant differences between sequences with a comfortable thumb-up and uncomfortable thumb-down final posture. Error bars represent standard errors after removal of between-subject variability (Cosineau, 2005).

4. Discussion

The present study examined whether *both* future goal postures (i.e., the sensitivity towards end-state comfort) and the possibility/impossibility to perform an action sequence are considered during motor imagery. Consistent with this notion, we found strikingly different RT patterns for the possible and impossible action sequences. Specifically, RTs and error rates increased almost monotonically with increasing angular disparity for the possible action sequences. However, slight deviations in RT monotonicity were evident when possible sequences contained an uncomfortable final posture. For these action sequences, RT values were significantly larger compared to the sequences that satisfied end-state comfort, but only at specific bar angular disparities (i.e., 90° cw and 135° ccw). In addition, mental rotation rates were also marginally slower for the possible sequences with an uncomfortable final posture than for the possible sequences with a comfortable final posture.

These results are congruent with the large corpus of work demonstrating that motor imagery is sensitive to biomechanical constraints (Jeannerod, 1994, 1995; Johnson, 2000; Parsons, 1987, 1994; Petit et al., 2003). While, for the possible sequences, the RT differences between comfortable and uncomfortable final postures were evident for the 90° and 135° angular disparity conditions, there were little to no differences in RTs for small angular disparities (<90°) and, interestingly, for the 180° angular disparity condition. This pattern fits nicely with a number of results from studies employing actual grasping in various bar-transport paradigms. Studies employing the original version of the bar-transport task usually report high percentages (>90%) of end-state comfort satisfaction (Hughes, Seegelke, Spiegel et al., 2012; Rosenbaum et al., 1990; Weigelt, Kunde, & Prinz, 2006). In contrast, lower end-state comfort satisfaction values (between 60% and 70%) are often reported when the bar-transport task is modified such that the object is initially oriented vertically and patients must rotate the object 180° (e.g., Hughes & Franz, 2008; Hughes, Seegelke, & Schack, 2012; Seegelke, Hughes, & Schack, 2011). Thus, a clear motor representation is established in actual grasping tasks in which end-state comfort is prioritized (i.e., 90° object rotation is required). Because this representation has been developed across the lifespan it can be more easily and quickly accessed than ESC-inconsistent representations. In contrast, there exists no favorable representation in actual grasping tasks in which end-state comfort is not prioritized (i.e., 180° object rotation is required, and consequently differences in RTs are not observed.

Compared to the possible to perform action sequences, a different pattern of results was observed for the impossible sequences. Specifically, RTs did not follow a mental rotation function typically observed (see Zacks & Michelon, 2005 for a review), but instead were uniformly very slow, and also not influenced by final posture.

Given that previous research has shown that people represent manual action sequences holistically in advance and are sensitive to the rotation requirements of the task (e.g., Hesse & Deubel, 2010; Seegelke, Hughes, Knoblauch, & Schack, 2013), we argue that participants in the present study compared the stimuli to a stored representation of the entire sequence and mentally simulated the action sequence. However, if this representation does not exist (as is presumed for a physically impossible to perform sequence since individuals lack actual physical experience performing such a sequence), participants do not mentally rotate the stimuli. Hence, an atypical mental rotation function is evident (see Petit & Harris, 2005 for similar results).

These findings also complement previous research indicating that information about the temporal movement organization (Güldenpenning, Koester, Kunde, Weigelt, & Schack, 2011; Güldenpenning, Kunde, Weigelt, & Schack, 2012) and the awareness of the ability to perform a sequential action (Bozzacchi, Giusti, Pitzalis, Spinelli, & Di Russo, 2012) are encoded in our motor representations. For example, using a response-priming paradigm, participants in Güldenpenning et al. (2011) were presented with target pictures showing body postures from the high-jump movement. The target pictures were preceded by prime pictures from the same movement and participants had to decide whether the target picture depicted the approach phase or the flight phase of the high-jump movement. The authors found that RTs were shorter for prime-target pairs that reflected the natural order of the movement (i.e., prime from approach phase, target from flight phase) compared to prime-target pairs that depicted the reversed order (i.e., prime from flight phase, target from approach phase). The authors argued that the temporal order effect reflects the activa-

Table 1
Mean error rates (in percent) as a function of bar angular disparity and sequence.

	Bar angular disparity							
	0°	45° ccw	45° cw	90° ccw	90° cw	135° ccw	135° cw	180°
Sequence								
Possible	1.4	2.6	3.3	4.1	7.4	7.4	6.2	8.7
Impossible	5.9	4.5	4.0	5.3	6.0	2.7	4.2	2.7

Table 2
Mean slopes (in ms/°), intercepts, correlations (*r*) as a function of final posture and sequence.

	Final posture					
	Thumb-up			Thumb-down		
	Slope	Intercept	*r*	Slope	Intercept	*r*
Sequence						
Possible	2.926	1150	0.386***	3.882	1128	0.332***
Impossible	−0.697	1686	0.075	−1.036	1716	0.115*

*** $p < .001$.
* $p < .05$.

tion of future aspects of the movement (i.e., prospective coding; Schütz-Bosbach & Prinz, 2007). Thus, participants anticipated the future course of the movement when presented with the prime picture, which ultimately led to either the facilitation when encoding the target picture (if prime-target pairs reflect the natural order, and hence a physically possible to perform action sequence) or to inference when encoding the target picture (if prime-target pairs reflect the reversed order, and hence a physically impossible to perform action sequence).

A similar conclusion can be derived from a study of Bozzacchi et al. (2012) who examined cortical activity (using EEG) during the preparatory phase of two goal-directed movements: grasping a tea-cup and impossible grasping of a tea-cup (same goal but the grasp was mechanically hindered by closing the fingers with a band). The authors noted prefrontal positivity that was present only during the preparation of an impossible grasping action but not during the preparation of a grasping or a reaching action. They reasoned that, on a neural level, the increased prefrontal activity during the preparation of an impossible grasping action compared to the preparation of a possible grasping action might reflect an inhibition of the goal or the awareness of being able to perform an action. In the present study, we speculate that, on a behavioral level, the increased reaction times for the impossible action sequences compared to the possible action sequence might reflect similar underlying cognitive processes.

In sum, the results of the present study indicate that both the possibility/impossibility to perform an action sequence and the sensitivity towards end-state comfort are considered during motor imagery. Thus, we suggest that motor representations contain information about the spatio-temporal movement organization and the awareness of being able to perform an action, which might be crucially involved in anticipation and planning of action sequences.

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