Exp Brain Res (2013) 224:447–454
DOI 10.1007/s00221-012-3324-0

RESEARCH ARTICLE

Constraining movement alters the recruitment of motor processes in mental rotation

David Moreau

Received: 12 September 2012 / Accepted: 25 October 2012 / Published online: 9 November 2012

Abstract Does mental rotation depend on the readiness to act? Recent evidence indicates that the involvement of motor processes in mental rotation is experience-dependent, suggesting that different levels of expertise in sensorimotor interactions lead to different strategies to solve mental rotation problems. Specifically, experts in motor activities perceive spatial material as objects that can be acted upon, triggering covert simulation of rotations. Because action simulation depends on the readiness to act, movement restriction should therefore disrupt mental rotation performance in individuals favoring motor processes. In this experiment, wrestlers and non-athletes judged whether pairs of three-dimensional stimuli were identical or different, with their hands either constrained or unconstrained. Wrestlers showed higher performance than controls in the rotation of geometric stimuli, but this difference disappeared when their hands were constrained. However, movement restriction had similar consequences for both groups in the rotation of hands. These findings suggest that expert's advantage in mental rotation of abstract objects is based on the readiness to act, even when physical manipulation is impossible.

Keywords Mental rotation · Motor processes · Sensorimotor expertise · Embodiment · Body posture

D. Moreau (✉)
Psychology Department, Princeton University,
Green Hall, Princeton, NJ 08544, USA
e-mail: dmoreau@princeton.edu

Introduction

Almost four decades ago, a landmark experiment by Cooper and Shepard demonstrated the similarities between mental rotation and physical rotation of hand stimuli (1975). Subsequent studies have confirmed these findings, showing that mental rotation of body parts is affected by anatomical constraints (Sekiyama 1982; Parsons 1987), and further refining the interdependency between motor properties and mental rotation (Parsons 1994; Pellizzer and Georgopoulos 1993; Georgopoulos and Massey 1987). Strongly established when dealing with representations of body parts, the involvement of motor processes in the rotation of geometrical or abstract figures is less evident. Pioneers in the study of motor processes in non-body rotations, Wohlschläger and Wohlschläger showed that mental rotation was facilitated by congruent hand movements (1998). In the same vein, Wexler and colleagues pointed out that reaction time decreased and accuracy improved when mental rotation matched manual rotation (Wexler et al. 1998). The apparent congruence between simultaneous covert and overt rotation does not seem to be caused by direct spatial equivalence between imagined and executed actions, as even a straightforward pulling movement resulting in the rotation of an object induced mental rotation facilitation (Schwartz and Holton 2000). In contrast with these findings (see for a meta-analysis and review Zacks 2008), several other neuroimaging studies have found no or little motor cortical activation in mental rotation tasks involving abstract objects (Vingerhoets et al. 2002; Kosslyn et al. 1998; Harris et al. 2000; Jordan et al. 2001).

One consistent explanation for such discrepancies lies within the malleability of strategies in mental rotation. A fascinating trend of research has demonstrated that strategies can be implicitly manipulated via the introduction of motor content, prior to or during mental rotation tasks (see for example Kosslyn et al. 2001). As such, a study by Wraga et al. demonstrated that performing a motor-related task resulted in subsequent activation of motor cortical areas in mental rotation of abstract objects, whereas these brain regions were not activated if the previous task consisted of non-body items (2003). This suggests that motor priming has immediate consequences on a subsequent set of actions, affecting strategy and processes recruitment.

Building on this idea, recent evidence showed that extensive experience in a motor activity triggered the involvement of motor processes in three-dimensional mental rotation, even when no motor priming was used (Moreau 2012). In this study, concurrent motor encoding disrupted mental rotation performance tremendously in subjects with substantial sensorimotor experience. In contrast, the control group was not affected to the same extent by a concurrent motor task, as individuals within this group seemed to rely strongly on visual encoding to manipulate objects mentally. These findings suggest that sensorimotor experience act as an implicit cue to trigger specific behavior in mental rotation problems. A related study complemented these findings, showing that sensorimotor expertise induces flexible strategies in mental rotation, whereas non-experts treat mental rotation stimuli consistently over time (Moreau et al. 2011).

This line of research indicates that the involvement of motor processes in reasoning tasks such as mental rotation depends on prior experience dealing with movements (Ferri et al. 2011, 2012), hence varying along a continuum rather than in an all-or-none fashion. Motor processes involvement in the manipulation of non-motor content is influenced by previous stimulation via movement-related content, whereas it is due to prior extensive experience (Moreau 2012) or more immediate and superficial exposure (Wraga et al. 2003).

These studies have demonstrated that the involvement of motor processes in mental rotation can be altered significantly. However, questions remain concerning the precise mechanisms underlying motor-based manipulation of spatial content. How does mental rotation benefit from motor processes? A plausible possibility is that motor priming leads to perceive spatial content as material that can be acted upon, within peripersonal space. Previous research has demonstrated that bringing objects within reach results in a dynamic mapping onto an egocentric frame of reference, via the process of action simulation, hence engaging motor processes in the mental manipulation of objects (Gallese 2005; Graziano 1999). Action simulation is a central component in various processes (Jeannerod 2001), therefore influencing numerous behaviors.

A compelling example comes from a recent study by Ambrosini et al. (2012). Recording participants' eye movements while they observed a grasping action, they showed that preventing an observer from the possibility to act, via movement restriction, resulted in impairments in gaze behavior. This study suggests that effective observation is based upon the ability to act (Ambrosini et al. 2012) and underscores the remarkable vulnerability of motor simulation to changes in body posture. Consistent with this idea, a series of studies by Ionta and colleagues showed that hand postures influence mental rotation of hands stimuli, suggesting that sensorimotor information plays a critical role in mental manipulation of body items (Ionta et al. 2007; Ionta and Blanke 2009). Having their hands behind their back or resting on their knees led to differences in participants' mental rotation performance, hence offering compelling arguments for a relationship between body posture and spatial visualization (Ionta et al. 2007). In line with a growing body of experimental evidence (Fourkas et al. 2006; Vargas et al. 2004), this studies yield clear evidence that even minor alterations in body posture induce changes in the readiness to act, with considerable consequences on motor simulation and therefore on mental rotation performance.

However, this trend of research concerned exclusively mental rotation of body parts. If action simulation is the covert process allowing higher performance of motor experts when manipulating abstract shapes (Moreau 2012), movement restriction should extend its disruptive effect to mental rotation of non-body items in motor experts but not in non-experts. This hypothesis is in line with the dynamic property of body mapping in sensory and motor cortices, which varies depending on body position in space (Graziano 2004) and objects' affordances (ter Horst et al. 2011).

More specifically, movement restriction should result in detrimental performance for all individuals when mental rotation involves body items. However, when presented with non-body items, only motor experts should be affected, as they rely on motor recoding of abstract shapes, whereas non-experts, who favor visual processes (Hyun and Luck 2007), should not be affected.

The aim of the present study was to test this set of hypotheses. To this purpose, expert wrestlers and non-athletes were recruited. They performed two mental rotation tasks while their possibility to move was either constrained or unconstrained. Wrestling was chosen for its propensity to induce embodied strategies in mental rotation, based on findings from prior studies (see for example Moreau 2012). Participants performed a mental rotation task that explicitly triggered motor processes involvement, using hand stimuli, and a mental rotation task that did not explicitly trigger motor strategies, using polygons.

Methods

Participants

A total of 32 right-handed participants with normal or corrected-to-normal vision volunteered in the present experiment (14 females; $M = 22.8$ years; range 19–27 years; SD = 2.42). Handedness was determined with the Hand Preference Test (Annett 1970). The study was conducted in accordance with the American Psychological Association Ethical Guidelines and with the Helsinki Declaration of 1975. Informed consent was obtained prior to participation.

The expert group consisted of 16 athletes (7 female, $M = 23.1$; SD = 2.54), who practiced wrestling at an elite level. The inclusion criterion for this group was to hold at least one selection for a national or international event at the time of the experiment. The control group consisted of 16 participants (7 female, $M = 22.6$; SD = 2.36), who did not practice any sport or physical activity on a regular basis. They had various athletic backgrounds, none of which could be qualified as regular practice in any physical activity, that is, sustained at least over a few months. None of the participants played a musical instrument, an activity that has been linked to high visuospatial abilities (Brochard et al. 2004).

Material and procedure

Participants performed two computerized, three-dimensional mental rotation tasks in two different conditions, with their hands either tied with a ribbon (constrained condition) or free (unconstrained condition), resting flat in front of them on a desk. A 2 (hand position) × 2 (order of presentation) repeated measures design was used, with half of the participants in each group randomly assigned to the Constrained condition first and the other half assigned to the Unconstrained condition first.

The experimental procedure was designed using E-Prime 2.0 (©Psychology Software Tools, Inc., 2010) and Java script editors. Participants sat approximately 70 cm away from a 17-inch computer screen. Every trial began with the presentation of a fixation cross. After 3,000 ms, the mental rotation task began. The two mental rotation tasks consisted of pairs of stimuli ($N = 25$) of either polygons or hands presented in a three-dimensional array (see Fig. 1). Participants had to decide whether the two stimuli were identical or different, by pressing a key with their right index ('G') or middle finger ('H'), respectively. The target figure, on the left of the screen, was presented at a randomly generated orientation, whereas the figure on the right was either a match or a mirror-image rotated by 45°, 90°, 135°, or 180° in one of the three axes (x, y, z). Stimuli remained visible until participants gave a response. After each response, participants had to press a key ('F') with their left index to proceed to the next problem. To ensure that hand positions were similar in the constrained and the unconstrained conditions, the three keys needed to perform the task were juxtaposed on the keyboard ('F', 'G', and 'H', corresponding to left index, right index, and right middle finger, respectively). This set of keys restricted the variability of hand positions in participants both within and between conditions, without the need to give explicit instructions related to hand movement. Hands were naturally juxtaposed, regardless of the condition (Constrained vs. Unconstrained), due to the set of keys needed to perform the tasks.

Both conditions started with the Polygon task, as prior studies have identified contamination effects when mental rotation of geometric shapes follows the manipulation of body parts stimuli (see for example Wraga et al. 2003). Participants were asked not to guess and to respond as soon

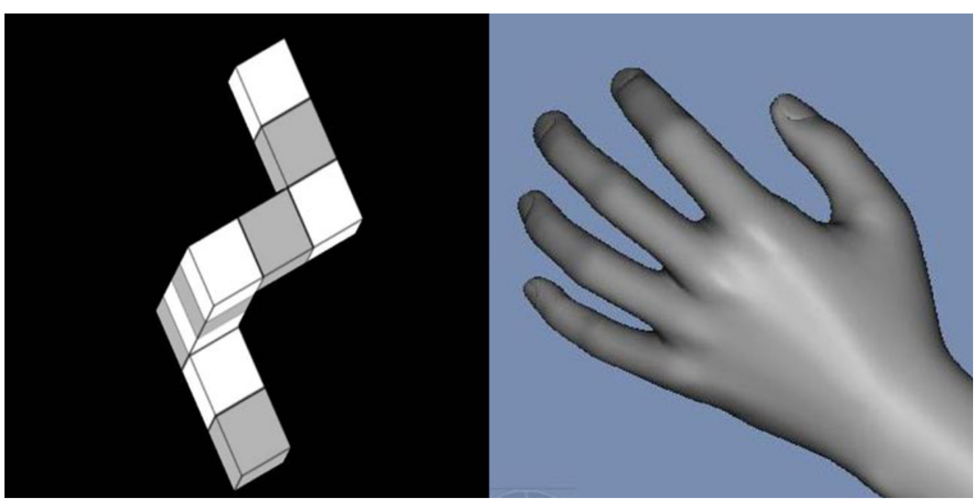

Fig. 1 Example stimuli from the Polygon task (*left*) and the Hand task (*right*)

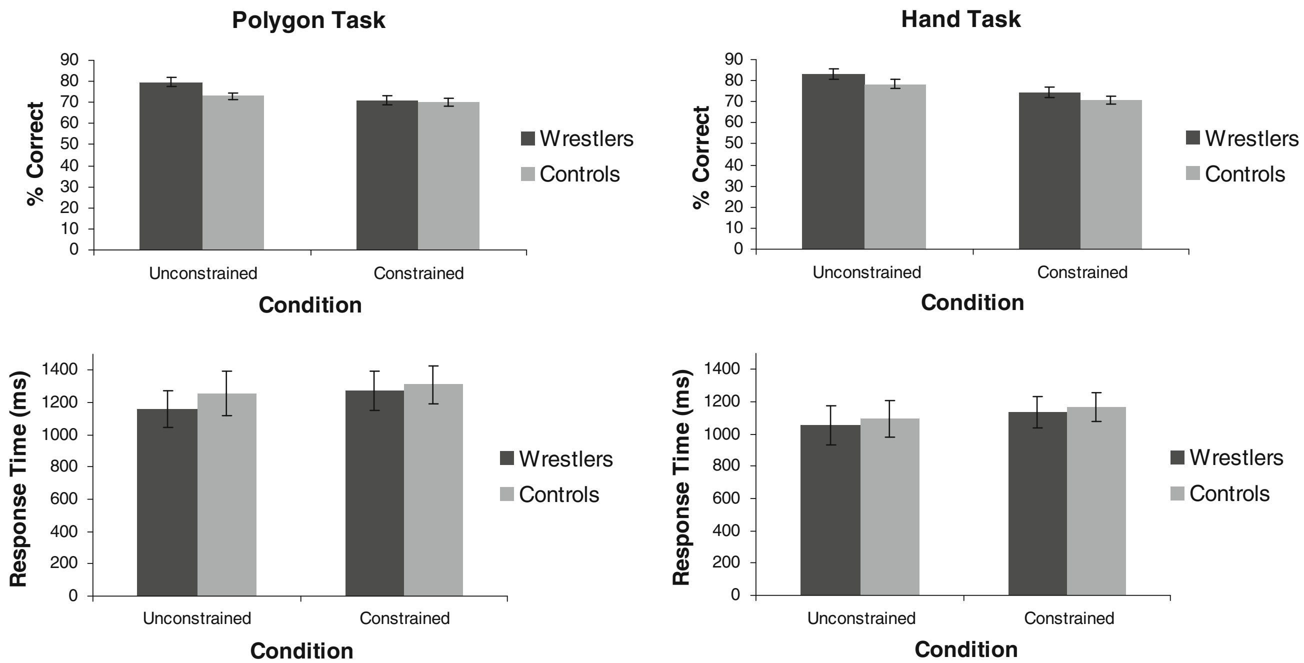

Fig. 2 Accuracy and response time for wrestler and control groups. *Error bars* represent standard errors of the means

as they were confident they had a correct answer. Accuracy and response time were recorded for each trial, and accuracy was subsequently quantified as percent correct.

Results

Figure 2 displays accuracy and response time for each condition, in the Polygon task and the Hand task. The results of a 2 (Motor Expertise) × 2 (Conditions) repeated measures ANOVA for each task are presented below.

Polygon task

The analysis of accuracy revealed a main effect of condition (Unconstrained, Constrained; $F(1,30) = 27.60$, $p < .001$, $\eta^2 = .48$) and a main interaction between motor expertise (Wrestlers, Controls) and condition ($F(1,30) = 7.51$, $p = .01$, $\eta^2 = .20$). Therefore, constraining movement affected wrestlers but not controls. Further, post hoc Tukey's HSD test showed that wrestlers outperformed controls when movement was not constrained ($M = 79.75$ %, SD = 8.94 and $M = 73.00$ %, SD = 7.08, respectively), but this effect disappeared when movement was constrained ($M = 71.00$ %, SD = 7.80 and $M = 70.25$ %, SD = 7.30, respectively). The analysis of response time did not show any significant effect, even after wrong answers were partialled out.

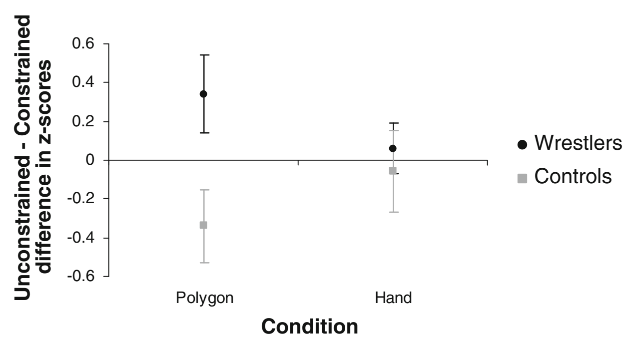

Fig. 3 Standardized accuracy score difference between Unconstrained and Constrained conditions, for Polygon and Hand tasks. *Error bars* represent standard errors of the means

Hand task

The analysis of accuracy revealed a main effect of condition ($F(1,30) = 49.40$, $p < .001$, $\eta^2 = .62$), but no significant interaction. Therefore, in contrast to the Polygon task, constricting movement in the Hand task had similar impact on mental rotation performance for wrestlers and controls (Unconstrained condition: $M = 74.75$ %, SD = 10.62 and $M = 70.75$ %, SD = 7.26, respectively; Constrained condition $M = 83.25$ %, SD = 10.04 and $M = 78.25$ %, SD = 8.64, respectively, see Fig. 3). Consistent with the Polygon task, the analysis of response time did not show any significant effect, even after wrong answers were partialled out.

Angular disparity

Although no effect of expertise was found in the Polygon or the Hand task response time data, differential effects of angular disparity could be underlying response time in the two groups. When response time was computed as a function of angular disparity (45°, 90°, 135°, 180°), a 2 (Motor Expertise) × 4 (Angular Disparity) ANOVA with repeated measures on the last variable was conducted for each condition in each task. As expected, the analyses showed main effects of angular disparity for each task and condition (all Fs > 30.00, all ps < .001). Post hoc comparisons (Tukey's HSD) showed differences in response time for both groups between all stimuli orientation, in both tasks and both conditions. However, there were no differences between wrestlers and controls, highlighting the loss of accuracy, but not speed, when movements are constrained. Response time data as a function of angular disparity for each task and condition are presented Fig. 4.

Control group median split

Wrestlers performed better than controls in the Polygon task when movement was not constrained. Therefore, it is possible that the differential effect we observed when constraining movement was due to differences in mental rotation ability, that is, high performers (wrestlers) suffered more than low performers (controls) from movement restriction. This would result in a larger dip in performance for wrestlers than controls and thus would explain the interaction effect yielded in the initial analysis. To discard this possibility and further specify the involvement of motor processes in mental rotation of polygons, the control group was divided between high and low performers following a median split around scores in the Unconstrained condition. Independent Student's test showed that the difference between low and high performers' correct responses remained significant in the Constrained condition (accuracy: $t(14) = 2.82$, $p < .05$). Thus, as opposed to the pattern of results differentiating wrestlers and controls, high and low performers within the control group were not affected differently by movement restriction when manipulating polygons.

Discussion

The aim of this experiment was to identify the mechanisms that allow sensorimotor experience to influence action simulation in mental rotation. To that purpose, wrestlers and non-athletes took two mental rotation computerized tasks in different conditions, with their hands either constrained or unconstrained. The rationale for this experimental setting was that constraining movements should affect readiness to act and thus action simulation, leading to impaired performance for individuals whose visualization during mental rotation is based upon motor processes.

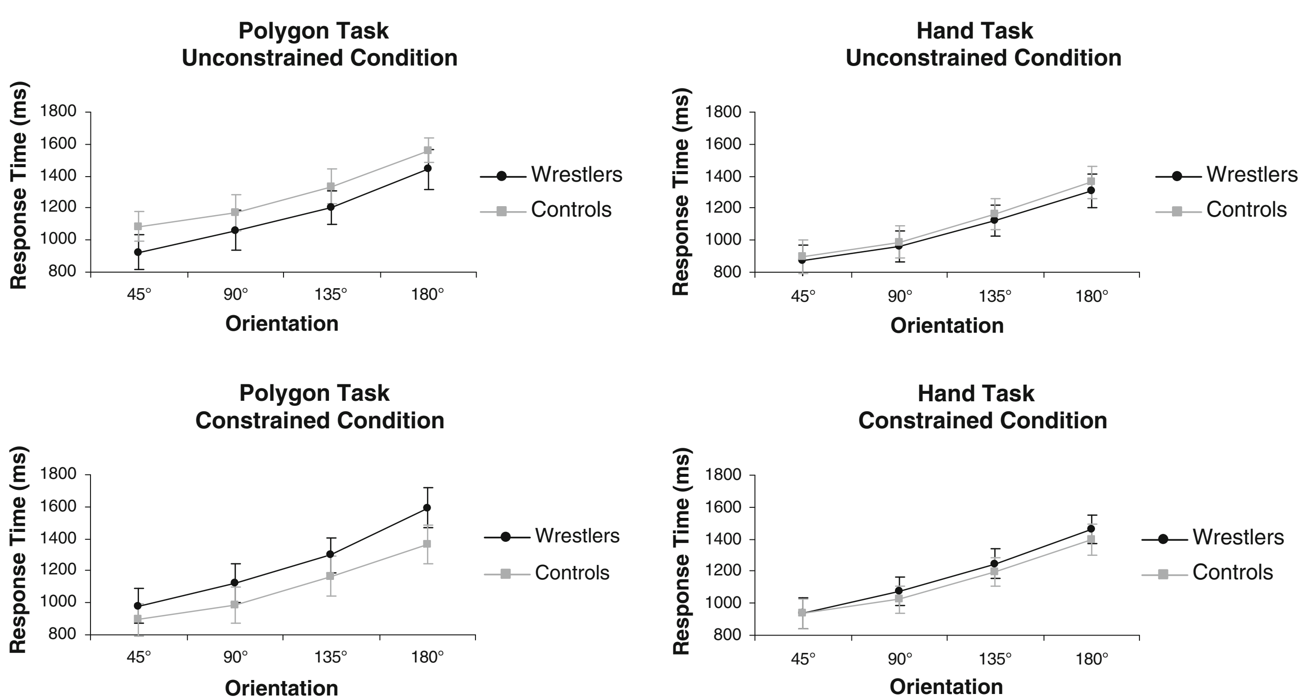

Fig. 4 Response time as a function of stimuli orientation for each task and condition. *Bars* represent standard errors of the means

Previous findings showing the effect of wrestling expertise on the mental manipulation of abstract objects were replicated (Moreau 2012; Moreau et al. 2011). More interestingly, the present study provides new insight concerning the mechanisms underlying the involvement of motor processes in mental rotation. Wrestlers showed higher performance than controls in the mental rotation task involving polygons, when movements were not constrained. However, their performance significantly dropped when hand movements were constrained, to a level matching controls' performance. Although this effect could be due to some kind of discomfort from being refrained to move, this is unlikely, as controls' performance was not altered by movement restriction. This finding is consistent with prior work showing the influence of hand posture on mental rotation (Ionta et al. 2007; Ionta and Blanke 2009), further refining the mediating role of sensorimotor experience in this process. Motor experts' advantage in mental rotation is highly malleable and can be altered via motor manipulation. Analyses on reaction time showed the usual linear increase in response time as a function of angularity, but did not follow the accuracy trend, as the large variance within groups participated in restricting the effects. One explanation for such an unpredicted finding could be the emphasis on accuracy over speed in the instructions given prior to testing. Participants knew responses were timed, but they were told that the primary focus was to give accurate answers. Thus, the emphasis on accuracy possibly resulted in a somewhat flatter distribution of reaction time scores across groups.

Interestingly, a different trend emerged when analyzing data concerning hand rotation. In these two conditions, wrestlers and controls did not differ, in overall accuracy or average response time. This suggests that when motor simulation is explicit, via hand stimuli, motor expertise might not be an advantage. However, when motor simulation is not explicitly suggested, as in the manipulation of polygons, sensorimotor experience allows engaging motor processes to solve problems in an efficient manner.

This interpretation naturally leads to the following question: why would both groups show similar results in the manipulation of hands, if wrestlers' superiority in dealing with polygons is based on motor processes? After all, mentally rotating hands seems more likely to induce embodied strategies than does rotating polygons. Despite the intuitive appeal of this assumption, there might be a more subtle explanation for the absence of significant group difference in the Hand task. In fact, it could reasonably be assumed that despite the extensive sensorimotor experience, wrestlers did not have more experience than controls dealing with the specific rotations of hands. In our everyday lives, we are exposed to others' hands in every orientation possible, and the ability to understand the meaning of gestures regardless of hand orientations is critical for successful social interactions. The occasions to become familiar with hand positions are therefore plentiful in a regular environment. Obviously, the assumption based on equivalent experience between groups also applies to the manipulation of polygons—wrestlers did not have more experience in mental rotation of geometric shapes per se—but the abstract features inherent to these figures were more likely to induce diverse and variable strategies, including motor recoding in the case of motor experts. Conversely, concrete depictions of hand stimuli might have refrained participants from substituting the actual shapes for a body-based equivalent, therefore leading them to prefer a strategy based on the actual hand pictures, in a process cognitively less demanding relative to any other kind of recoding.

The analysis conducted after separating high and low mental rotation performers within the control group complemented these findings. As opposed to the difference between wrestlers and controls, high and low performers within the control group were not affected differently when hand movement was constrained, high performers outscoring low performers significantly. Therefore, the difference observed between wrestlers and controls when movement was constrained is not one of the mental rotation abilities per se, but of the underlying processes recruited to perform the task.

As pointed out in the Method section, all participants started with the Polygon task, to avoid contamination effects from body-based item to geometric stimuli. Thereby, a possibility that cannot be ruled out is that practice effects allowed general improvements in mental rotation problems for all groups. Assuming that wrestlers were already experts in mental rotation due to extensive experience dealing with physical bodies in three-dimensional space, their margin of improvements could have been relatively limited, as opposed to controls' high potential increases. This could have allowed for a reduction of the variance between groups, with controls reaching up to wrestlers' performance. Despite this limitation, the present experiment undoubtedly highlights that the involvement of motor processes, besides depending on sensorimotor experience, rests upon the possibility to act. These two prerequisites—experience and potential action—need to be present to allow efficient processing based on motor strategies. As such, motor simulation depends on the possibilities offered by a given situation, which encompass both individual abilities and environmental settings.

At first sight, the present findings do not seem compatible with Chu and Kita's work advocating for the internalization of motor strategies in mental rotation as sensorimotor experience increases (Chu and Kita 2008, 2011). In their three-stage model, individuals first solve mental rotation problems by physical manipulation of an object. Progressively, physical manipulation becomes "deagentivized", that is, gestures do not need to be performed on a particular object. Finally, rotation becomes internalized and does not rely on actual movement (Chu and Kita 2008). Because of their high performance in mental rotation, one could suppose that experts in motor activities have reached that final stage and therefore that they would not be affected by physical restriction. The internalization of spatial representations would result in more permanent and stable changes, relatively immune to simple motor constraints. However, rather than challenging this view, the present findings specify how the incapacity to act disrupts motor-based strategies in mental rotation. Extensive sensorimotor experience leads to more efficient and internalized strategies in spatial manipulation, yet this dynamic process depends on reasonable possibilities and potential outcomes within the real world, susceptible to physical changes. In that sense, these findings are consistent with previous work showing detrimental effects in performance when mental rotations are physically impossible, especially in the face of biomechanical constraints (Petit et al. 2003).

Although less plausible than the one detailed herein, it should be noted that an alternative explanation for the present findings exists. Neurophysiological studies in animals have shown that changes in forelimb position alter motor cortical output representations, hence emphasizing the dynamic and location-dependent features of motor cortical mappings (Sanes et al. 1992; Graziano 2004). Following this line of work, the differential effects observed in the present study could have been caused by changes in arm or hand positions, rather than in the possibility to act per se. Different positions would produce different consequences on cortical mapping of motor areas, therefore leading to changes in terms of motor system recruitment. Although theoretically plausible, this explanation is unlikely because arm positions in Constrained and Unconstrained conditions were closely matched via constraints on the set of keys required to respond. Further work should complement these findings using controlled changes in limb position and in the possibility to act, varying independently from each other, in order to separate their respective role in mental rotation.

In addition, the present study demonstrates that motor manipulation leads to a decrease in performance for individuals favoring motor strategies, therefore emphasizing the tremendous benefits of motor strategies in mental rotation tasks along with the remarkable susceptibility of their implementation. In this sense, the paper provides further evidence for a tight relationship between cognitive and motor processes, consistent with the embodied approach of cognition.

Acknowledgments The author is thankful to Dr. Peters, University of Guelph, Canada, for providing the MRT stimuli library (Peters and Battista 2008).

Conflict of interest The author declares that he has no conflict of interest.

References

Ambrosini E, Sinigaglia C, Costantini M (2012) Tie my hands, tie my eyes. J Exp Psychol Hum Percept Perform 38(2):263–266

Annett M (1970) A classification of hand preference by association analysis. Br J Psychol 61:303–321

Brochard R, Dufour A, Despres O (2004) Effect of musical expertise on visuospatial abilities: evidence from reaction times and mental imagery. Brain Cogn 54(2):103–109. doi:10.1016/S0278-2626(03)00264-1

Chu M, Kita S (2008) Spontaneous gestures during mental rotation tasks: insights into the micro development of the motor strategy. J Exp Psychol Gen 137(4):706–723

Chu M, Kita S (2011) The nature of gestures' beneficial role in spatial problem solving. J Exp Psychol Gen 140(1):102–116. doi:2011-01710-004

Cooper LA, Shepard RN (1975) Mental transformations in the identification of left and right hands. J Exp Psychol Hum Percept Perform 104(1):48–56

Ferri F, Frassinetti F, Costantini M, Gallese V (2011) Motor simulation and the bodily self. PLoS ONE 6(3):e17927

Ferri F, Frassinetti F, Ardizzi M, Costantini M, Gallese V (2012) A sensorimotor network for the bodily self. J Cogn Neurosci 24(7):1584–1595

Fourkas AD, Ionta S, Aglioti SM (2006) Influence of imagined posture and imagery modality on corticospinal excitability. Behav Brain Res 168:190–196

Gallese V (2005) Embodied simulation: from neurons to phenomenal experience. Phenomenol Cogn Sci 4:23–48

Georgopoulos AP, Massey JT (1987) Cognitive spatial-motor processes. 1. The making of movements at various angles form a stimulus direction. Exp Brain Res 65:361–370

Graziano M (1999) Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. Proc Natl Acad Sci USA 96:10418–10421

Graziano M (2004) Mapping from motor cortex to biceps and triceps altered by elbow angle. J Neurophysiol 92:395–407

Harris IM, Egan GF, Sonkkila C, Tochon-Danguy HJ, Paxinos G, Watson JD (2000) Selective right parietal lobe activation during mental rotation: a parametric PET study. Brain 123(1):65–73

Hyun JS, Luck SJ (2007) Visual working memory as the substrate for mental rotation. Psychon Bull Rev 14(1):154–158

Ionta S, Blanke O (2009) Differential influence of hands posture on mental rotation of hands and feet in left and right handers. Exp Brain Res 195:207–217

Ionta S, Fourkas AD, Fiorio M, Aglioti SM (2007) The influence of hands posture on mental rotation of hands and feet. Exp Brain Res 183(1):1–7. doi:10.1007/s00221-007-1020-2

Jeannerod M (2001) Neural simulation of action: a unifying mechanism for motor cognition. Neuroimage 14:103–109

Jordan K, Heinze HJ, Lutz K, Kanowski M, Jancke L (2001) Cortical activations during the mental rotation of different visual objects. Neuroimage 13(1):143–152. doi:10.1006/nimg.2000.0677

Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM (1998) Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 35(2):151–161

Kosslyn SM, Thompson WL, Wraga M, Alpert NM (2001) Imagining rotation by endogenous versus exogenous forces: distinct neural mechanisms. NeuroReport 12(11):2519–2525

Moreau D (2012) The role of motor processes in three-dimensional mental rotation: shaping cognitive processing via sensorimotor experience. Learn Individ Differ 22(3):354–359

Moreau D, Mansy-Dannay A, Clerc J, Guerrien A (2011) Spatial ability and motor performance: assessing mental rotation processes in elite and novice athletes. Int J Sport Psychol 42(6): 525–547

Parsons LM (1987) Imagined spatial transformations of one's hands and feet. Cogn Psychol 19:178–241

Parsons LM (1994) Temporal and kinematic properties of motor behavior reflected in mentally simulated action. J Exp Psychol Hum Percept Perform 20(4):709–730

Pellizzer G, Georgopoulos AP (1993) Common processing constraints for visuomotor and visual mental rotation. Exp Brain Res 93: 165–172

Peters M, Battista C (2008) Applications of mental rotation figures of the Shepard and Metzler type and description of a mental rotation stimulus library. Brain Cogn 66(3):260–264. doi: S0278-2626(07)00144-3

Petit LS, Pegna AJ, Mayer E, Hauert CA (2003) Representation of anatomical constraints in motor imagery: mental rotation of a body segment. Brain Cogn 51(1):95–101. doi:10.1016/s0278-2626(02)00526-2

Sanes JN, Wang J, Donoghue JP (1992) Immediate and delayed changes of rat motor cortical output representation with new forelimb configurations. Cereb Cortex 2(2):141–152

Schwartz DL, Holton DL (2000) Tool use and the effect of action on the imagination. J Exp Psychol Learn Mem Cogn 26(6): 1655–1665

Sekiyama K (1982) Kinesthetic aspects of mental representations in the identification of left and right hands. Percep Psychophys 32:89–95

ter Horst AC, van Lier R, Steenbergen B (2011) Spatial dependency of action simulation. Exp Brain Res 212:635–644

Vargas CD, Olivier E, Craighero L, Fadiga L, Duhamel JR, Sirigu A (2004) The influence of hand posture on corticospinal excitability during motor imagery: a transcranial magnetic stimulation study. Cereb Cortex 14:1200–1206

Vingerhoets G, de Lange FP, Vandemaele P, Deblaere K, Achten E (2002) Motor imagery in mental rotation: an fMRI study. Neuroimage 17(3):1623–1633

Wexler M, Kosslyn S, Berthoz A (1998) Motor processes in mental rotation. Cognition 68(1):77–94

Wohlschläger A, Wohlschläger A (1998) Mental and manual rotation. J Exp Psychol Hum Percept Perform 24:397–412

Wraga M, Thompson WL, Alpert NM, Kosslyn SM (2003) Implicit transfer of motor strategies in mental rotation. Brain Cogn 52(2):135–143. doi:S0278262603000332

Zacks JM (2008) Neuroimaging studies of mental rotation: a meta-analysis and review. J Cogn Neurosci 20(1):1–19