

**The Motor-Cognitive Model of Motor Imagery:
Evidence from Timing Errors in Simulated Reaching and Grasping**

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Abstract

Motor imagery represents an important but theoretically underdeveloped area of research in psychology. The Motor-Cognitive Model of motor imagery was presented, and contrasted with the currently prevalent view, the Functional Equivalence Model. In three experiments, the predictions of the two models were pitted against each other through manipulations of task precision and the introduction of an interference task, while comparing their effects on overt actions and motor imagery. In Experiments 1a and 1b, the Motor-Cognitive Model predicted an effect of precision whereby motor imagery would overestimate simulated movement times when a grasping action involved a high level of precision; this prediction was upheld. In Experiment 2, the Motor-Cognitive Model predicted that an interference task would slow motor imagery to a much greater extent than it would overt actions; this prediction was also upheld. Experiment 3 showed that the effects observed in the previous experiments could not be due to failures to match the motor imagery and overt action tasks. None of the above results were explainable by either a strong version of the Functional Equivalence Model, or any reasonable adaptations thereof. It was concluded that the Motor-Cognitive Model may represent a theoretically viable advance in the understanding of motor imagery.

Public Significance Statement

Understanding motor imagery has important implications for its use in therapeutic interventions, as well as in understanding the human mind. The present paper presents the Motor-Cognitive Model of motor imagery. Three experiments were reported that found that motor imagery can be more affected by task precision and interference from secondary tasks than overt actions, consistent with this theory but not with the currently popular Functional Equivalence Model.

The Motor-Cognitive Model of Motor Imagery:

Evidence from Timing Errors in Simulated Reaching and Grasping

Research on motor imagery has helped reveal the neural and functional bases of action representation, perception, and production (Aflalo et al., 2015; Macuga & Frey, 2012; Vogt, Di Rienzo, Collet, Collins, & Guillot, 2013). Motor imagery represents a valuable tool in motor skill training and rehabilitation (Blair, Hall, & Leyshon, 1993; Denis, 1985; Hummelsheim, 1999), and shows great promise as a therapy for neurological disabilities (Grabherr, Jola, Berra, Theiler, & Mast, 2015; Harris & Hebert, 2015). However, previous work on motor imagery has focussed almost entirely on empirical research with little attention directed towards theoretical development (Guillot & Collett, 2005; Guillot, Hoyek, Louis, & Collet, 2012; Moran, Guillot, Macintyre, & Collett, 2012). Yet given its clear relevance across numerous fields, it would seem advantageous to have a robust, detailed theory of motor imagery.

In a first step towards such a theory, we here present the Motor-Cognitive Model of motor imagery. We describe its behavioral and neurological bases, and contrast it with a currently prevalent view, here referred to as the Functional Equivalence Model (Decety, 1996; Jeannerod, 1994). We believe the Motor-Cognitive Model offers two main theoretical advantages over the Functional Equivalence Model: First, the Motor-Cognitive Model explains the neural and behavioral differences as well as similarities between motor imagery and overt actions, whereas the Functional Equivalence Model explains only the similarities. Second, the Motor-Cognitive Model offers straightforward, easily testable predictions regarding the circumstances under which overt and imagined actions should either match or differ. This again contrasts with the Functional Equivalence Model, a strong version of which predicts only matches across all conditions. Following an evaluation of the behavioural and neurological evidence, we report three experiments that reveal systematic discrepancies in the timing of motor imagery relative to overt actions; these are as predicted by the Motor-Cognitive Model, but not the Functional Equivalence Model. We conclude that the Motor-Cognitive Model represents a potentially useful theoretical framework for understanding motor imagery.

The Motor-Cognitive Model of Motor Imagery

Put succinctly, the Motor-Cognitive Model argues that central executive functions play an important role in motor imagery that is not evident in overt actions. To reach this conclusion, the Motor-Cognitive Model begins with the well-established distinction between action planning and control (Elliott, Helsen, & Chua, 2001; Glover, 2004; Meyer, Abrams, Kornblum, Wright, & Smith, 1988; Woodworth, 1899). Just as with overt actions, motor imagery is argued to be a two-stage process involving both pre-movement planning and realtime execution. Prior to beginning a simulated action, an initial motor image is generated based on the same stored motor representations as are used to plan overt actions, and at the planning stage motor imagery and overt actions are functionally and neurologically matched. During execution, however, the two behaviours diverge. Whereas overt actions access unconscious and automatic visual and proprioceptive feedback processes in conjunction with a forward model to monitor and fine-tune the movement in flight (Cameron, Enns, Franks, & Chua, 2009; Glover, 2004; Goodale, Pelisson, & Prablanc, 1986; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Pisella et al., 2000), motor imagery is unable to utilize such processes in the absence of physical movement. In place of online control, the unfolding motor image is monitored, and to varying degrees elaborated in real time, through a conscious executive control process that must also switch attention between the motor image and the action being used to index it (e.g., a button press or verbal response). In brief, during execution overt actions use unconscious online control whereas motor imagery uses conscious executive control.

The elaboration and monitoring of motor imagery in real time relies on a central pool of executive resources, similar to their use in working memory (Nieuwenstein & Wyble, 2014; Rademaker, Bloem, De Weerd, & Sack, 2015). The amount of resources required for these functions depends heavily on the fidelity of the motor representations used to generate the initial motor image. Highly developed motor representations, such as those that are available for overpracticed and/or more ballistic actions, may support a motor image that represents the physical outcome of an action with high fidelity; these images unfold with relatively little conscious elaboration. Such high fidelity images place low demands on the central resource pool, resulting in an easy switching of attention between motor imagery and the response used to index it, and leading to simulated actions that closely match the characteristics of their overt counterparts.

In contrast, poorly developed motor representations, such as those that exist for novel actions and/or actions that rely heavily on online control, lead to the initial generation of a motor image of low fidelity. This low fidelity imagery results in a heavy reliance on conscious elaboration during execution. The need to consciously generate large parts of the motor image heavily taxes the central resource pool, which delays the switching of attention between the motor image and its indexing response. This ultimately results in motor imagery taking longer than its corresponding overt action (e.g., Gandrey, Paizis, Karathanasis, Gueugneau, & Papaxanthis, 2013).

An example of a task associated with a highly developed motor representation would be pointing to a large, stationary target. In this case, the internal representation of the action would have a high fidelity with the overt movement, which itself would be largely ballistic. With access to a high fidelity representation, the motor image of this action would require little conscious elaboration. As a result, motor imagery should only lightly tax the executive resource pool, making it easy to switch attention between the motor image and the indexing response. Under these conditions, motor imagery should closely simulate the timing of an action. In contrast, pointing to a small, randomly moving target would be an action with a much greater reliance on online control, and as a corollary, a much less developed internal motor representation (as the action itself is much less ballistic and much more online in nature). The result would be a low fidelity image, and the elaboration of the motor image in this case would heavily tax conscious executive resources. This in turn would impair the switching of attention between the image and the response used to index it, and would ultimately lead to longer movement times for motor imagery relative to the corresponding overt action.

Similar to the behavioral component of the model, neurologically the Motor-Cognitive Model posits a match between motor imagery and overt action during planning and a bifurcation during execution. Both motor imagery and overt action activate the same frontoparietal and subcortical circuits prior to initiation, but during execution overt action relies on nearby though more dorsal regions to update an ongoing movement (Glover, 2004; Glover, Wall, & Smith, 2012). In contrast, the central pool of executive resources used to monitor the unfolding of a motor image utilize a network centred on the dorsolateral prefrontal cortex (Dux, Tombu, Harrison, Rogers, Tong, & Marois, 2009). Motor imagery may also employ early visuo-perceptual areas of the occipital lobe and ventral visual stream to help elaborate the visual elements of an image (Guillot, Collett, Nguyen, Malouin, Richards, & Doyon, 2008).

To summarise, the Motor-Cognitive Model posits that during planning, motor imagery is behaviorally and neurologically matched with overt actions. During execution, motor imagery and overt action diverge, with motor imagery relying on the executive resource pool to elaborate the motor image and to switch attention between this process and the response used to index it. The resource pool has a role in motor imagery inversely proportionate to the fidelity of the motor representations used to generate the image. The less fully these representations are able to simulate the movement, the greater the emphasis placed on the use of executive resources to develop the image, and in turn, the more difficulty there is in switching attention between these processes and the execution of the indexing response. Overtaxing of the resource pool thus results in longer movement times by motor imagery relative to overt action. In contrast, high fidelity images created through the use of strong motor representations place less emphasis on the use of executive resources, which are able to then easily switch attention between the motor image and the indexing response, which in turn allows motor imagery to accurately simulate the timing of the overt action.

The Functional Equivalence Model of Motor Imagery

The Functional Equivalence Model contrasts with the Motor-Cognitive Model in being much simpler in its explanation of motor imagery. Unlike the Motor-Cognitive Model, this model does not assume any differences between motor imagery and overt action during execution, but instead assumes that the ongoing motor image simply represents the unfolding of the motor representation in the absence of overt movement (Decety, 1996; Jeannerod, 1994). As such, motor imagery should utilize the same neural regions that are active during the planning of overt actions, and should closely match its behavioral outputs. With a strict reliance on motor representations for both the generation and execution of motor imagery, and with no theoretical necessity for conscious image generation or executive monitoring, the Functional Equivalence Model predicts that motor imagery should be able to accurately simulate actions across a broad range of circumstances. In contrast to the Motor-Cognitive Model then, the Functional Equivalence Model does not predict any systematic timing errors in motor imagery, nor any systematic differences in neural activation patterns between motor imagery and overt actions.

Behavioral Evidence Favors the Motor-Cognitive Model

Motor imagery often accurately simulates the time taken to execute actions across a variety of tasks, including pointing (Decety & Michel, 1989; Watson & Rubin, 1996), writing (Papaxanthis, Pozzo, Skoura, & Schieppati, 2002; Tumas & Sakamoto, 2009), locomotion (Saimpont, Malouin, Tousignant, & Jackson, 2012) and sporting activities (MacIntyre & Moran, 1996; Oishi, Kasai, & Maeshima, 2000). Motor imagery and overt actions show similar effects of various cognitive variables such as word labels and visual illusions (Glover, Dixon, Castiello, & Rushworth, 2005; Glover & Dixon, 2013), and both generally adhere to Fitts' Law (Cerritelli, Maruff, Wilson, & Currie, 2000; Decety & Jeannerod, 1995; Macuga & Frey, 2014; Macuga, Papailiou, & Frey, 2012; Maruff, Wilson, DeFazio, Cerritelli, Hedt, & Currie, 1999; Sirigu, Cohen, Duhamel, Pillon, Dubois, Agid, & Pierrot-Deselligny, 1995; but see Young, Pratt, & Chau, 2008). All of this evidence is consistent with both the Motor-Cognitive Model and the Functional Equivalence Model.

However, timing errors also occur in motor imagery that can only be explained by the Motor-Cognitive Model. For example, motor imagery often takes longer than the corresponding overt action when simulating novel and/or less ballistic movements (Calmels & Fournier, 2001; Cerritelli, Maruff, Wilson, & Currie, 2000; Decety, Jeannerod, & Prablanc, 1989; Slifkin, 2008). Moreover, practice with the overt action systematically decreases these effects in motor imagery (Chandrasekharan, Binsted, Ayres, Higgins, & Welsh, 2012; Yoxon, Tremblay, & Welsh, 2015). Less commonly, motor imagery may have shorter movement times than the simulated action. This can occur in conditions which contrast with those resulting in longer imagery times, such as overlearned or highly practiced movements (Calmels & Fournier, 2001; Grealy & Shearer, 2008; Hanyu & Itsukushima, 2000). An elegant study by Calmels, Holmes, Lopez, & Naman (2006) revealed the effects of both overpracticed and relatively novel elements of action on the timing of motor imagery. Elite gymnasts were asked to imagine a complex vaulting manoeuvre, and to indicate verbally when they had completed a) the run-up to the apparatus, and b) the vault itself. Participants' imagery times were shorter than the time needed to complete the overlearned aspect of the movement (the run-up), but longer than the time required to complete the relatively novel aspect (the vault).

Although the Functional Equivalence Model does not predict or explain any such discrepancies between the timing of motor imagery and overt actions, the Motor-Cognitive Model does. On the one hand, motor representations for novel actions such as the vault are poorly developed, and their overt execution would rely heavily on online control processes.

For motor imagery, the elaboration of the image as a result requires much greater conscious involvement, taxing the central resource pool, and delaying the response used to index motor imagery. The motor representations for overpracticed actions such as the run-up to the apparatus have a high fidelity with the overt action. As such, the initial motor image is vivid, requires little or no conscious development online, and can be simulated at the same or even a greater speed than the corresponding action.

To recap, the review of behavioral evidence is consistent with the Motor-Cognitive Model, which holds that imagining novel or otherwise difficult actions that require a greater reliance on online control will lead to longer imagery times than are required to perform the corresponding action (Calmels & Fournier, 2001; Cerritelli, Maruff, Wilson, & Currie, 2000; Decety, Jeannerod, & Prablanc, 1989; Rieger, 2012; Slifkin, 2008). At least some of the underestimations that occur when the action being simulated is overpracticed (Calmels & Fournier, 2001; Calmels et al., 2006) are also in line with the Motor-Cognitive Model. These mismatches are difficult to reconcile with the Functional Equivalence Model, however, which holds that by utilizing the same internal processes as overt actions, motor imagery should closely match their timing.

Neurological Evidence Favors the Motor-Cognitive Model

Both motor imagery and overt action planning tend to activate a broad network of frontal, parietal, and subcortical regions (Hetu et al., 2013; Jeannerod, 2001; Miller et al., 2010), an overlap previously taken as support for the Functional Equivalence Model (Decety, 1996; Jeannerod, 1994). However, several neurological dissociations also exist between motor imagery and overt action: First, the strength of the activation in a particular area often differs between motor imagery and overt action. For example, whereas both behaviors tend to be associated with increased activity in the SMA and M1, activity in the SMA is greater during motor imagery than overt action, whereas activity in M1 is greater during overt action and lesser or absent during motor imagery (see Hetu et al., 2013, for a review), a fact often attributed to the need to inhibit overt actions in motor imagery. Second, increases in activation during motor imagery can occur in regions outside of the classic motor areas (Dietrich, 2012; Filimon, Nelson, Hagler, & Sereno, 2007; Gerardin, Sirigu, Lehericy et al. (2000; Macuga & Frey 2012; Nair, Purcott, Fuchs, Steinberg, & Kelso, 2003), consistent with the Motor-Cognitive Model but not the Functional Equivalence Model. Areas specific to motor imagery include ventral stream visual areas of the occipital and temporal lobes (Guillot, et al., 2009; Jiang, et al., 2015), and areas of the frontal lobes associated with

executive processes including the inferior frontal gyrus and dorsolateral prefrontal cortex (Guillot, Collet, Nguyen, Malouin, Richards, & Doyon, 2009). Consistent with the role of executive processes in elaborating low fidelity motor images, activation of the inferior frontal gyrus during motor imagery is significantly greater in persons who are poor at imagining movements than in those who are skilled (Guillot et al., 2009), and is also greater in persons imagining novel movements (Olsson & Nyberg, 2011).

Brain injury or disease also can lead to dissociations between motor imagery and overt action that can only be explained as resulting from differences in their neural organisation (see McInnes, Friesen, & Boe, 2015, for a review). For example, Sirigu et al. (1995) reported that parietal patients showed mismatches in the timing of motor imagery and overt actions (cf. Danckert, Ferber, Doherty, Steinmetz, Nicolle, & Goodale, 2002). A similar result was found after cerebellar damage (Grealy & Lee, 2011), and a number of other neurological disorders, including Parkinson's Disease (Cohen, Chao, Nutt, & Horak, 2011), multiple sclerosis (Tacchino et al., 2013), and clinical depression (Bennabi et al., 2014), have been shown to coincide with discrepancies between motor imagery and overt action. In sum, the neurological evidence also favors the Motor-Cognitive Model over the Functional Equivalence Model. Only the former predicts the differences in neural activation patterns and the existence of neuropsychological dissociations between motor imagery and overt actions. For example, the Motor-Cognitive Model predicts the activation of inferior frontal and prefrontal executive areas during motor imagery as supporting the process of image generation and monitoring. In contrast, the Functional Equivalence Model would predict a much nearer coincidence of neural processes involved in motor imagery and overt action, as well as closely matching effects of neurological deficits (Jeannerod, 1994).

Overview of the Present Study

We here report a set of experiments designed to test the contrasting predictions of the Motor Cognitive and Functional Equivalence Models. In Experiments 1a and 1b, we conducted the first empirical test of the effects of varying the precision requirements of a reaching and grasping task on motor imagery. Participants had to either execute or imagine executing two tasks that varied in terms of the amount of precision required, and hence their reliance on online control. We predicted, in line with the Motor-Cognitive Model, that imagined movement times would lengthen more than overt movement times when there was an increased the emphasis on online control. The alternate prediction provided by the Functional Equivalence Model was that imagined and overt movement times would be

similar in both the high and low precision variants of each task. To anticipate, increasing precision had a greater effect on imagined than on overt movement times in Experiments 1a and 1b, supporting the Motor-Cognitive Model but not the Functional Equivalence Model.

Experiment 2 used another novel approach to the study of motor imagery. Here, participants were required to execute or imagine executing the same high/low precision task as in Experiment 1b, but in some conditions had to simultaneously perform a backwards counting task known to utilize executive resources. According to the Motor-Cognitive Model, such an interference task should significantly impair the ability of participants to generate and monitor motor imagery and to switch attention to the indexing response; the consequence should be a large increase in imagined movement times in the counting condition relative to the no-counting condition. Simultaneously, little or no such effects on movement times should occur for overt actions, as the execution of these rely on unconscious visual and proprioceptive feedback processing rather than on executive monitoring. In contrast, the Functional Equivalence Model would posit that the interference task should have identical effects on both motor imagery and overt action. Our results showed that the interference task had a very large effect on the timing of motor imagery coupled with a relatively small effect on the timing of overt action, again consistent with the Motor-Cognitive Model but not the Functional Equivalence Model.

Finally, Experiment 3 was designed to control for a possible confound in the previous experiments, specifically the requirement of participants in the motor imagery condition to index the timing of their imagery with button presses, and the presence of a computer keyboard in the action space. Closely matching the overt action condition to the motor imagery condition in Experiment 3 led to the same pattern of results as in the previous experiments; motor imagery was again more affected by precision and the secondary counting task than was overt action. This result confirmed that the previous results were not simply an artefact of the tasks used to measure motor imagery and overt actions.

Experiment 1a

Experiment 1a examined the effects of task precision and the reliance on online control on motor imagery. In Experiment 1a, one group of participants reached to and grasped an egg and lifted it from a holder, whereas another group imagined executing the same movement. The surface of the egg could be either coated in butter (high precision

condition), or uncoated (low precision condition). Previous work has shown that the time taken to reach to and grasp an object with a low-friction surface is longer than that for an otherwise identical object with a high-friction surface (Fikes et al., 1994), most likely due to an increased reliance on online control to ensure a stable grasp (Glover, 2004). In line with this, we expected kinematic analysis to show a greater reliance on online control in the high precision than low precision condition for the overt movement, as evidenced by longer deceleration times and a greater number of online adjustments (Elliott et al., 2001).

According to the Motor Cognitive Model, the greater emphasis on online control in the high precision condition should result in a lower fidelity motor representation, and hence an increased reliance on conscious image generation and monitoring during motor imagery. This should in turn lead to a delay in switching attention between the motor image and the indexing response, resulting in longer imagery movement times than overt action movement times in the high precision condition only. This should be evident in an interaction between group (overt action vs. motor imagery) and precision (high vs. low) such that the effect of increasing precision should be greater on imagery than on overt action. In contrast, the Functional Equivalence Model would predict that motor imagery, relying entirely on the same motor representations as are used by overt action, should not show a systematic timing effect in either the high or low precision variants of the task, and as such, no such interaction between task type and precision should occur.

Method

Participants

Thirty participants sampled from the campus of Royal Holloway University of London took part in both Experiments 1a and 1b in return for a small monetary reward. Participants were randomly assigned to the overt action group or the motor imagery group, and all participants completed both Experiments 1a and 1b in a single session lasting approximately 30 minutes. The use of separate groups in the motor imagery and overt action conditions ensured that participants could not use tacit knowledge of their performance in the latter task to guide performance in the former (Pylyshyn, 2002). There were six males and nine females in the overt action group (mean age 25 years) and five males and ten females in the motor imagery group (mean age 24 years). All participants had normal or corrected vision, were right-handed by self-report, and had no motor or neurological impairments. All

gave informed consent prior to testing, and all were naïve as to the exact purpose of the study. The experimental protocol was approved by the Psychology Departmental Ethics Committee at Royal Holloway University of London.

Stimuli and Apparatus

Figure 1 shows the set-up for Experiment 1a. Participants were seated at the long side of a (120 x 80cm) rectangular table. A starting mark was positioned 8 cm from the table edge, aligned with the participants' sagittal plane. Stimuli consisted of an egg situated in an upright position in a white plastic convex egg cup holder anchored to the table with an adhesive, such that the centre of the egg was 24 cm directly in front of, and approximately 5 cm higher than the starting location. Two equally-sized eggs were used in the experiment (approximately 5 cm in width at their widest point and 9 cm in height). The more oblong portion of the egg was placed inside the holder. The egg cup holder contained the bottom 1.4 cm of the egg. In the high-precision condition the surface of the egg was coated in butter, whereas in the low-precision condition the egg had no coating.

For the overt action group, a Polhemus Fastrak system was used to record movements. This involved attaching a sensor (7 mm in diameter) to the nail of the thumb of the right hand using surgical tape. The sensor cable was taped to the participant's right forearm to provide further support and stability. For the motor imagery group, the Polhemus sensors were replaced with a keyboard set on the table to the left of the starting position, with its right edge approximately 10 cm from the starting location. Participants held their left index finger on the 'j' key of the keyboard throughout each trial. The 'j' key was approximately 25cm left of, 8cm in front of, and 2cm in height above the starting position of the right hand.

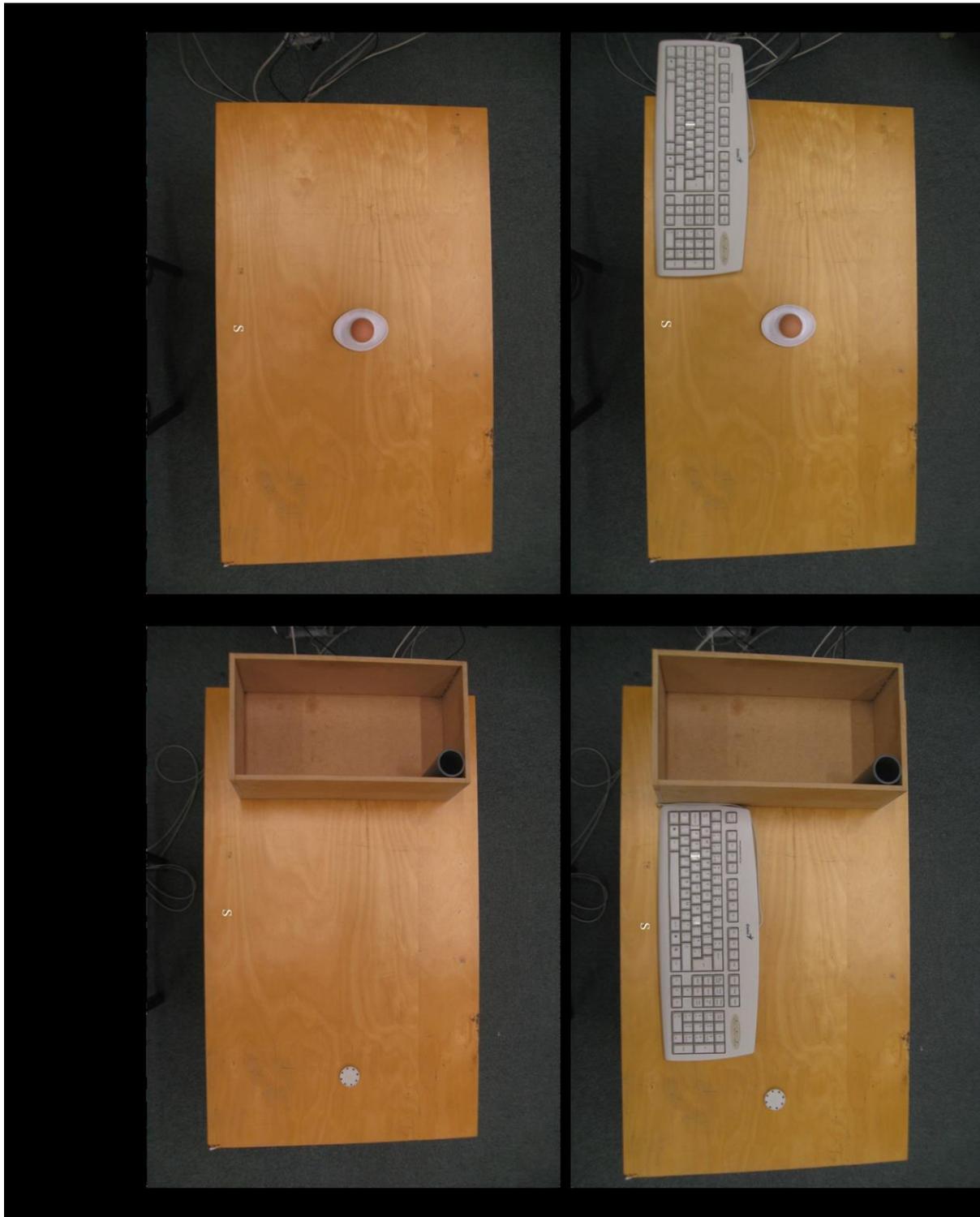


Figure 1. Top-down view of the layout for Experiments 1, 2, and 3. Top left: motor imagery condition, Experiment 1a. Bottom left: overt action condition, Experiment 1a. Top right: motor imagery condition, Experiment 1b, 2, and 3, and overt action condition: Experiment 3. Bottom right: overt action condition, Experiments 1b and 2. 'S': starting position for right hand. 'I': key used for indexing response with the left hand.

Procedure

All participants began each trial sitting at the table with the thumb and finger of their right hand in contact with the starting position. The sounding of a tone activated through the PC by the experimenter indicated the beginning of each trial. At the tone, the overt action group was required to reach out and grasp the egg and lift it completely out of its holder using only the thumb and index finger of the right hand, before placing it back down in the holder again. Participants were instructed to move as quickly as possible without dropping the egg. They kept their left hand in their lap in a comfortable position throughout each trial. The Polhemus recorded the instantaneous x, y, and z position of the sensors at 120 Hz and data were recorded to PC for analysis offline. Errors were recorded when participants either moved early or failed to lift the egg successfully; these trials were repeated.

For the motor imagery group, the sounding of the tone indicated that they were to imagine reaching out to grasp the egg and lift it out of its cup, again as quickly as possible but without dropping it, and to indicate the initiation of the movement, contact with the egg, and lifting of the egg through three consecutive presses of the 'j' key on the keyboard. The three presses were used to avoid confusion over when the critical reaching to grasp movement directed at the egg was completed. The timing between the first and second presses (i.e., the imagined movement time of reaching to and grasping the egg) were recorded onto PC for analysis offline. Participants were instructed to keep their right hand immobile in the starting position throughout each trial. Errors were recorded when participants pressed a key too early or inadvertently moved their right hand; these trials were repeated.

There were eight repetitions of each precision condition, presented in a blocked, ABBA design. For eight of the participants, the first four trials were high-precision, the next eight low-precision, and the final four high-precision, with the opposite pattern used for the other seven participants. Following a block of high-precision trials, participants in the overt action group were given a napkin to wipe their hands. The experimenter also wiped his hands before touching the uncoated egg. Following the full session (both experiments), participants were asked which condition (coated vs. uncoated egg) they found more difficult.

Design and Analysis

Kinematic data in the overt action group were analysed using a custom program designed to measure movement time. Data were first passed through a Gaussian filter at 70 Hz to smooth any recording artefacts. The instantaneous velocity of the thumb was then computed for each 8.25 msec interval. The time between movement onset and offset was recorded as movement time. Movement onset was defined as the first of five consecutive intervals during which velocity exceeded 0.05 cm/s. Movement offset was determined as the local velocity minima between the velocity peak of the reaching to grasp movement and the velocity peak of the subsequent lifting movement. Peak velocity between movement onset and offset was determined from the thumb velocity, and from this we split each movement into the times spent in acceleration (prior to peak velocity) and deceleration (post peak velocity). Finally, we measured the number of online adjustments as the number of re-accelerations in the velocity profile in the deceleration phase.

Two sets of statistical analyses were conducted. First, a mixed ANOVA was used to measure the effects of precision (high vs. low) and group (overt action vs. motor imagery) on imagined and overt movement times. In this analysis, precision was a repeated measure, task type was a between-subjects measure, and participants were treated as a random variable. Second, for the overt action group only, t tests were used to compare time spent in the acceleration phase, time spent in the deceleration phase, and the number of online adjustments, in the high and low precision conditions respectively.

Results

Figure 2 shows the effects of group (overt action vs. motor imagery) and precision condition on imagined and overt movement times. Although there was no main effect of group, $F [1, 14] = 1.18, p > 0.05$, there was a main effect of precision, with overall longer times associated with the high precision condition, $F [1, 14] = 22.38, p < 0.001, \eta^2 = .37$. Critically, and in line with the Motor-Cognitive Model but not the Functional Equivalence Model, there was an interaction between the precision and group conditions, with the difference in movement times for the precision conditions being greater in the imagery group than in the overt action group, $F [1, 14] = 4.60, p < 0.05, \eta^2 = .17$. Specifically, there was a longer mean imagery movement time than overt action movement time in the high precision condition only.

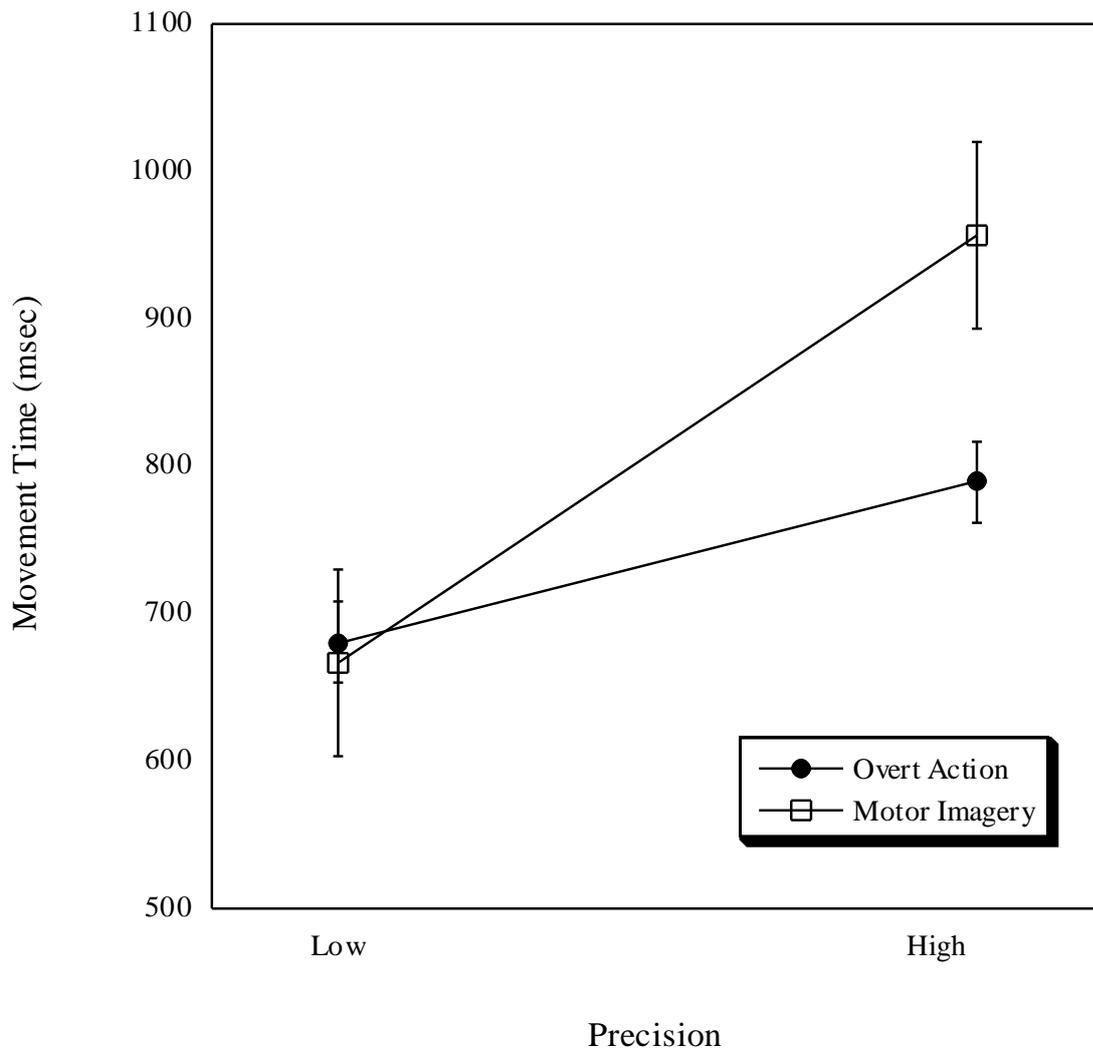


Figure 2. Effects of precision on imagined and overt movement times in Experiment 1a. Error bars represent standard errors of the mean.

Kinematic data from the overt action group are summarized in Table 1. Whereas time spent in the acceleration phase was unaffected by precision, $t(14) = 1.70, p > 0.05$, both time spent in the deceleration phase, $t(14) = 2.25, p < 0.05$, and the number of online adjustments, $t(14) = 3.74, p < 0.01$, were greater in the high precision than in the low precision condition. Taken in sum, these results show that our manipulation worked: the high precision condition placed a greater emphasis on online control than the low precision condition. Participants

spent more time in the deceleration phase, and made more online adjustments, in the high precision condition relative to the low precision condition.

Table 1

Comparison of mean kinematic parameters in the high precision versus low precision conditions of Experiment 1a in the overt action group (standard errors in parentheses).

Kinematic Variable	High Precision (slippery egg)	Low Precision (control egg)
Acceleration Time (msec)	206.18 (8.03)	194.37 (8.18)
Deceleration Time (msec)	583.36 (38.18)	486.18 (33.96)
Online Adjustments	3.56 (0.25)	2.33 (0.23)

Experiment 1b

In a previous study, Marteniuk et al. (1987) reported that the precision requirement of the second movement in a sequence affected the kinematics and movement times of the initial reach and grasp of the target (cf. Gentilucci et al., 1997). The movement made to grasp the object took longer, and had a longer deceleration phase, when the subsequent movement involved placing the object into a small cylinder than when it involved tossing it into a large box. In Experiment 1b, we adapted this task to compare the effects of manipulating precision on overt action and motor imagery. Participants in the overt action group reached to and grasped a circular disc and then either placed it into a small cylinder (high precision

condition) or tossed it into a large box (low precision condition), whereas the same movements were simulated mentally by participants in the motor imagery group. This thus provided a converging test of the effects of precision on motor imagery timing. As we'd assumed for Experiment 1a, we also assumed here that the high precision placing task would result in a greater emphasis on online control processes than the low precision tossing task.

Both the Motor-Cognitive Model and the Functional Equivalence Model made the same predictions as for Experiment 1a. According to the Motor-Cognitive Model, the greater difficulty of the placing task should have a greater effect on imagined movement times than on overt movement times, resulting in an interaction between precision and group. In contrast, the Functional Equivalence Model predicted that motor imagery should accurately simulate the times required to complete the actions in both conditions, resulting in no such interaction.

Method

Participants

The same thirty participants who took part in Experiment 1a also performed Experiment 1b. Participants remained in the same group (overt action or motor imagery) for the second experiment, which ran consecutively with the first in a single session. Participants were not told the purpose of either experiment until the entire session was completed, after which they were fully debriefed.

Stimuli and Apparatus

Figure 1 (right panels) shows the set-up for the tossing/placing task. Experiment 1b used the same table and starting position as Experiment 1a. Here, the stimuli were a white plastic disc (4 cm in diameter and 1 cm thick), positioned with its centre 32 cm to the right and 10 cm forward of the starting position. To the left of the participant was situated a 15 cm high, 4.2 cm diameter solid grey plastic tube, centred 47 cm left and 40 cm forward of the starting position, placed inside of a 42 x 22 x 15.7 cm (height) wooden box, centred 56 cm to the left and 21 cm forward of the starting position. In the motor imagery condition, the keyboard was present directly in front of the starting position, but participants in Experiment 1b used the 'd' key on the keyboard rather than the 'j' key, as this was now in a more

comfortable location for their finger to rest on owing to the different placement of the keyboard. The 'd' key was approximately 15 cm to the left of, and 9 cm in front of, the starting position.

Procedure

The procedure was the same as in Experiment 1a, except that the task was to reach to grasp the disc and then either place it in the cylinder or toss it in the box. As in Experiment 1a, the order of precision condition was blocked using an ABBA design, with an initial four trials in one condition followed by all eight trials of the other condition, followed by the final four trials of the first condition. Eight participants began with the tossing condition, seven with the placing condition. In the motor imagery group (Figure 1, top right), participants had to press the 'd' key once when they imagined initiating the movement, again when they imagined grasping the disc, and again when they imagined placing/tossing it into the target receptacle. Imagined movement times for the initial reach-to-grasp of the block were recorded as the time between the first and second button presses. In the overt action group (Figure 1, bottom right), participants had to reach to grasp the disc and either place it in the cylinder (high precision condition) or toss it in the box (low precision condition).

Design and Analysis

Design and analysis were identical to Experiment 1a.

Results

Figure 3 depicts the effects of group (overt action vs. motor imagery) and precision condition on imagined and overt movement times. As in Experiment 1a, there was a main effect of precision condition, $F [1, 14] = 28.15, p < 0.001, \eta^2 = .44$. Unlike Experiment 1a, there was also a main effect of group, with movement times being longer overall in the imagery than in the overt action group, $F [1, 14] = 8.24, p < 0.01, \eta^2 = .13$. Finally, as predicted by the Motor-Cognitive Model but not the Functional Equivalence Model, an interaction was present whereby the effect of precision was greater on motor imagery than on

overt action, $F [1, 24] = 4.64$, $p < 0.05$, $\eta^2 = .07$.

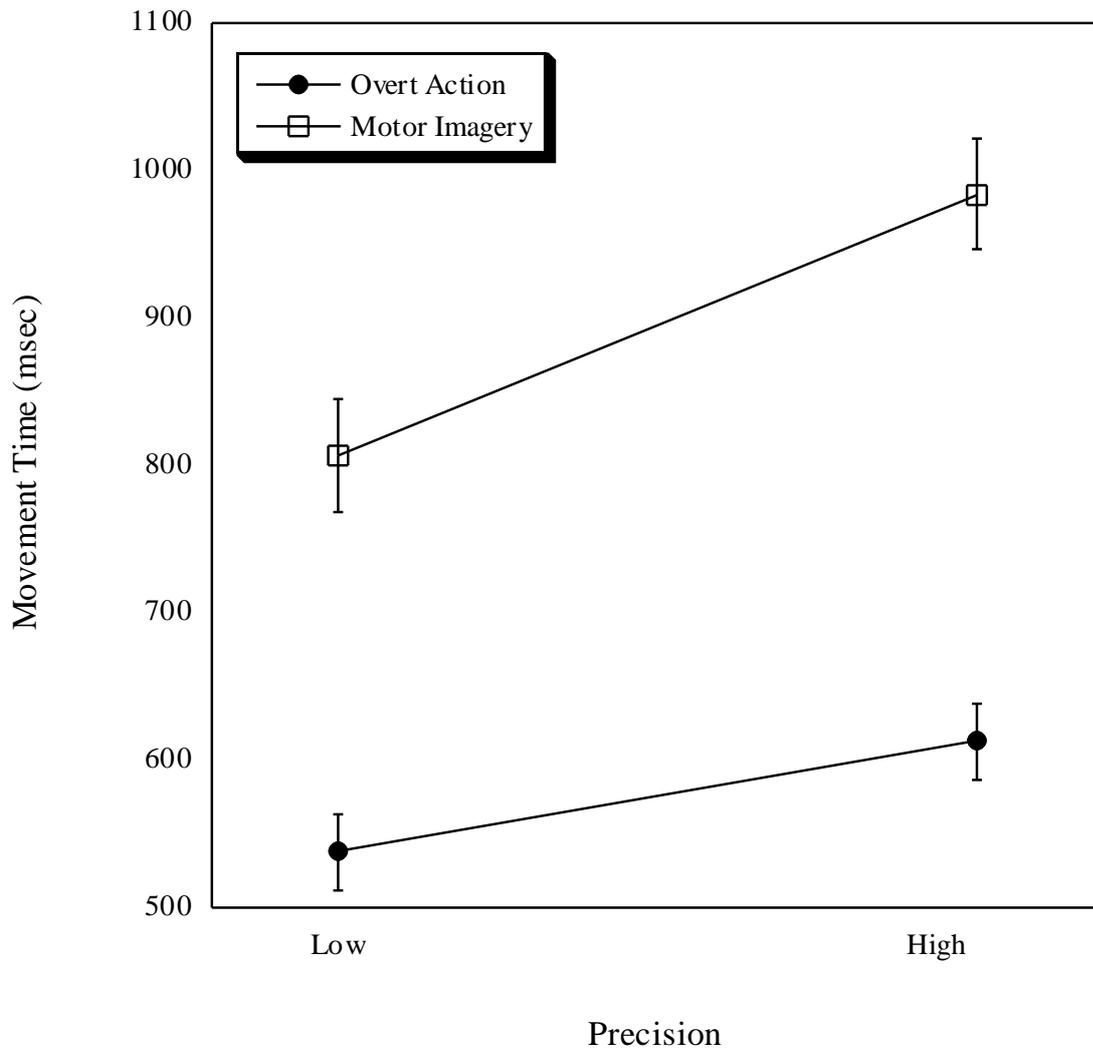


Figure 3. Effects of precision on imagined and overt movement times in Experiment 1b. Error bars represent standard errors of the mean.

To confirm that precision affected online control, we again analysed the kinematic data of the overt action condition (Table 2). As in Experiment 1a, time spent in the acceleration phase did not differ across precision, $t (14) = 1.33$, $p > 0.05$. However, both the time spent in the deceleration phase, $t (14) = 2.64$, $p < 0.05$, and the number of online adjustments, $t (14) = 1.96$, $p = 0.07$, were greater in the high precision than low precision condition, although the evidence for the latter effect was marginal.

Table 2

Comparison of mean kinematic parameters in the high precision versus low precision conditions of Experiment 1b in the overt action group (standard errors in parentheses).

Kinematic Variable	High Precision (grasping-to-place)	Low Precision (grasping-to-toss)
Acceleration Time (msec)	204.05 (9.83)	189.78 (8.64)
Deceleration Time (msec)	408.97 (40.81)	348.34 (30.87)
Online Adjustments	2.25 (0.30)	1.77 (0.21)

Discussion

There were two main findings of Experiments 1a and 1b. First, our premise that the high precision task would place a greater emphasis on online control than would the low precision task was upheld. Second and more importantly, whereas participants in both the overt action and motor imagery groups had longer movement times in the high precision condition than in the low precision condition, the increase was greater in the imagery group than in the overt action group. This interaction was as predicted by the Motor Cognitive Model, but not the Functional Equivalence Model.

A discrepancy in the results of these experiments was the overall effect of task group on movement times. Specifically, participants in the motor imagery group of Experiment 1b had longer movement times than did those in the overt action group, whereas no such group effect was observed in Experiment 1a. On reflection, we suspected that this may have

resulted from an unforeseen artefact in the experimental design. In the motor imagery group, the task of imagining grasping and moving the object to the receptacle was complicated by the presence of the keyboard directly in front of the participants. As participants had to imagine moving the hand over this potential obstacle, this may have caused the increase in imagined movement times for the initial grasping movement. No such interference would have occurred in Experiment 1a, as the keyboard was placed to the left of the starting position, nor in the overt action task of Experiment 1b, wherein the keyboard was not present. We address this issue further in Experiment 3. Despite this possible complication, however, the critical result remained: precision had a greater effect on motor imagery than on overt action.

Whereas Experiments 1a and 1b showed consistently that task difficulty affected motor imagery in a different way than overt actions, they were limited inasmuch as they focussed on manipulations of the same task variable of precision. Therefore, to provide a further test of the Motor-Cognitive Model and the Functional Equivalence Model, we next conducted an experiment that compared the effects of an interference task on the timing of motor imagery and overt action.

Experiment 2

Experiment 2 used the same reaching-to-grasp and tossing/placing task as Experiment 1b, but with the inclusion of an interference task designed to draw on the central pool of executive resources. According to the Motor-Cognitive Model, during the execution of motor imagery, elaboration of the motor image and the switching of attention between imagery and its indexing response are monitored by a central pool of resources. If the Motor-Cognitive Model is correct, it ought to be possible to disrupt the timing of motor imagery by including a task that interferes with the use of this resource pool. Conversely, overt action does not use this pool during execution, and thus should not be affected by its concurrent use in another task. The result should be an interaction between group and counting conditions. In contrast, the Functional Equivalence Model holds that motor imagery relies entirely on the use of stored motor representations shared with overt action. As such, there should be no reason to think that motor imagery would be affected by inclusion of an interference task unless it also affects overt action. In other words, the Functional Equivalence Model predicts equivalent effects of the interference task on both overt action and motor imagery, and thus no interaction between group and counting conditions.

In Experiment 2 we also measured the secondary movement of tossing/placing the disc into the box/cylinder. We expected this second measure to be affected by precision and interference in a manner similar to the initial reach-to-grasp of the disc, and thus analyzing both parts of the movement sequence would provide a more robust evaluation of the data.

Method

Participants

A new group of 30 participants, all introductory psychology students at Royal Holloway University of London, took part in Experiment 2 in return for course credit. Participants were randomly assigned to either the overt action group or the motor imagery group, and completed the experiment in a single session lasting approximately 20 minutes. There were three males and twelve females in the overt action group (mean age 19 years) and two male and thirteen females in the motor imagery group (mean age 19 years). All participants had normal or corrected vision, were right-handed by self-report, and had no motor or neurological impairments. All gave informed consent prior to testing, and all were naïve as to the exact purpose of the study. The experimental protocol was approved by the Psychology Departmental Ethics Committee at Royal Holloway University of London.

Stimuli and Apparatus

Experiment 2 used the same apparatus as Experiment 1b (Figure 1, right panels).

Procedure

The procedure was identical to that of Experiment 1b, except that on half of the trials participants were required to complete the motor imagery or overt action task while simultaneously counting backwards out loud by threes. The starting numbers were pseudorandomly generated between the values of 51-99, inclusive, and were read to participants by the experimenter just prior to trial onset. On the other half of trials, participants were required to complete the motor imagery or overt action task without counting backwards, as had been done in Experiment 1b. The order of counting/non-counting trials was blocked with place/toss conditions in an ABBA design so that eight of the

participants completed the counting task first while either placing or tossing, followed by the non-counting trials of the same type, followed by the non-counting trials in the other condition (place vs. toss, whichever had not been done previously), followed by the counting trials in the other condition. The other seven participants did the counting/non-counting blocks in the opposite order.

Design and Analysis

Design and analysis were similar to Experiments 1a and 1b, with the addition of counting vs. no counting as a within-subjects variable. Additionally, we recorded the kinematic, imagined and overt movement times for not just the initial reach to grasp of the disc (or time between first and second button presses in the motor imagery group), but also for the tossing/placing movement (or time between second and third button presses in the motor imagery group). Overt action / motor imagery was again a between-subjects variable. The result was two 2x2x2 mixed ANOVAs of movement time, one for each step of the movement. For the kinematic variables of time in acceleration phase, time in the deceleration phase, and number of online corrections, we conducted six 2x2 ANOVAs, one per measure in each step of the movement, with counting/no-counting and high/low precision as repeated measures.

Results

The first ANOVA examined the initial reach-to-grasp movement of the disc (Figure 4). There were longer movement times in the motor imagery vs. overt action condition, $F [1, 28] = 22.33, p < 0.001, \eta^2 = .44$, in the high precision vs. low precision condition, $F [1, 28] = 22.29, p < 0.001, \eta^2 = .30$, and in the counting vs. no counting condition, $F [1, 14] = 37.45, p < 0.001, \eta^2 = .26$. The interaction between precision and counting was also significant, $F [1, 14] = 4.63, p < 0.05, \eta^2 = .02$, with counting affecting movement times more in the high precision condition than in the low precision condition.

Most importantly, as predicted by the Motor-Cognitive Model but not the Functional Equivalence Model, there was a significant interaction between the group and counting conditions, $F [1, 28] = 24.89, p < 0.001, \eta^2 = .17$, with counting having a much larger effect on motor imagery than on overt action. Also consistent with the Motor-Cognitive Model was the significant interaction between group and precision, $F [1, 28] = 8.22, p < 0.001, \eta^2 = .11$,

with precision affecting motor imagery more than overt action. Finally, although there was some tendency for the effects of counting and precision on group to be additive, the three-way interaction was insignificant, $F [1, 14] = 1.36, p > 0.10$.

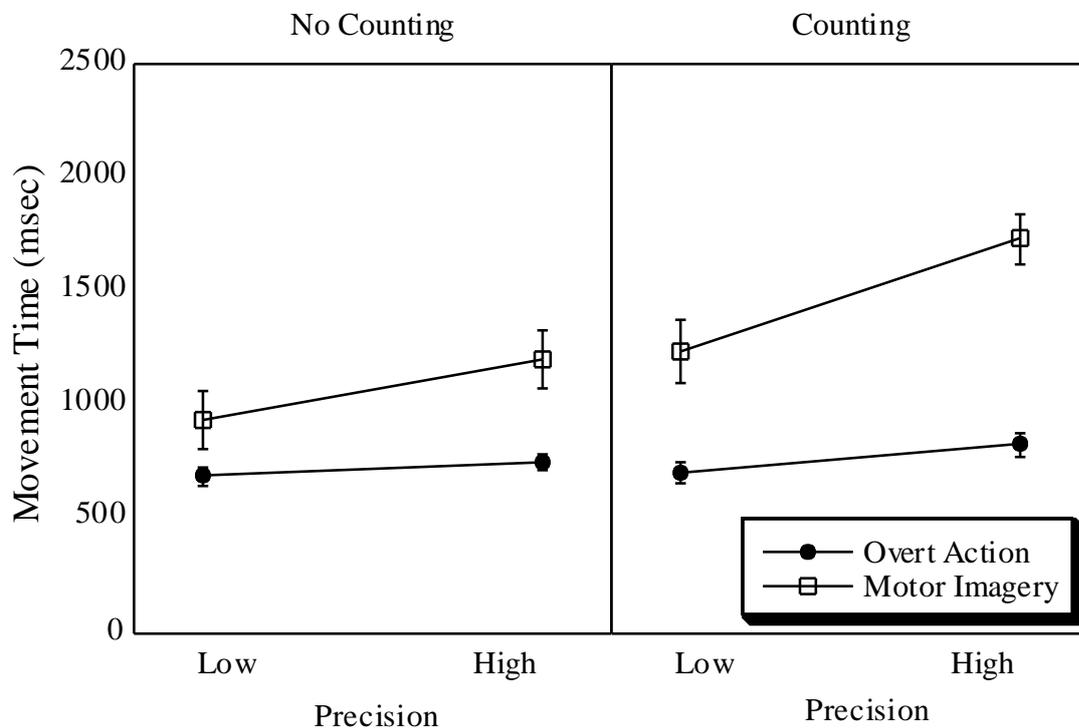


Figure 4. Effect of precision and counting on imagined and overt movement times in the initial reach-to-grasp of the disc in Experiment 2. Left: No counting condition. Right: Counting condition. Error bars represent standard errors of the mean.

The second ANOVA examined movement times in the tossing/placing portion of the movement (Figure 5). Movement times were longer in the motor imagery vs. overt action condition, $F [1, 14] = 36.46, p < 0.001, \eta^2 = .44$, in the high precision vs. low precision condition, $F [1, 14] = 65.81, p < 0.001, \eta^2 = .55$, and in the counting vs. no counting conditions, $F [1, 14] = 22.15, p < 0.001, \eta^2 = .15$. There was also a significant interaction whereby the effect of precision was greater in the counting vs. no counting condition, $F [1, 14] = 9.40, p < 0.01, \eta^2 = .04$.

Again, as predicted by the Motor-Cognitive Model but not the Functional Equivalence Model, the critical interaction between the group and counting conditions was significant, $F [1, 14] = 12.90, p < 0.01, \eta^2 = .09$, with counting affecting motor imagery more than overt action. The predicted interaction between group and precision was also present, $F [1, 14] = 14.20, p < 0.01, \eta^2 = .06$, with the effect of increasing precision being much greater on motor imagery than on overt action. Finally, there was evidence in this portion of the action that the effects of precision and counting on motor imagery were additive, with the three-way interaction being significant $F [1, 14] = 4.92, p < 0.05, \eta^2 = .07$.

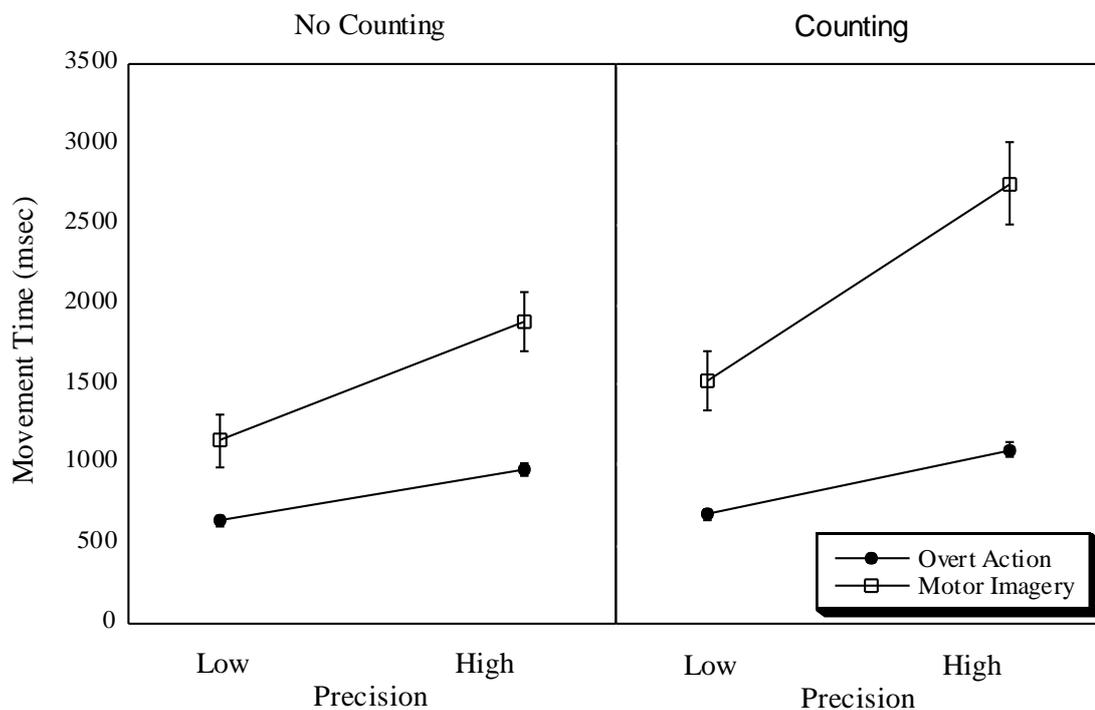


Figure 5. Comparison of precision and counting effects on imagined and overt movement times in the second phase of the movement in Experiment 2 (low-precision tossing versus high-precision placing). Error bars represent standard errors of the mean.

The final six ANOVAs for Experiment 2 examined the effects of counting and precision on kinematics in the first and second movement, respectively, for the overt action group; data are summarized in Table 3.

Table 3

Comparison of mean kinematic parameters in the high precision versus low precision conditions of Experiment 2 in the overt action group. All values in milliseconds (standard errors in parentheses).

Kinematic Variable

Phase 1 (reaching-to-grasp)	No counting	No counting	Counting	Counting
	High Precision	Low Precision	High Precision	Low Precision
Acceleration Time (msec)	241.27 (13.98)	254.28 (17.93)	270.65 (19.27)	259.89 (19.11)
Deceleration Time (msec)	505.41 (21.82)	431.09 (24.72)	558.46 (34.69)	438.24 (28.54)
Online Adjustments	3.83 (0.28)	2.65 (0.22)	3.63 (0.18)	2.58 (0.17)

Phase 2 (tossing/placing)	No counting	No counting	Counting	Counting
	High Precision	Low Precision	High Precision	Low Precision
Acceleration Time (msec)	296.06 (12.22)	244.55 (12.50)	342.43 (14.13)	254.07 (15.28)
Deceleration Time (msec)	673.04 (21.55)	402.88 (16.68)	740.31 (29.30)	435.71 (19.30)
Online Adjustments	4.12 (0.37)	1.62 (0.15)	3.88 (0.21)	1.75 (0.16)

For the initial reach-to-grasp of the disc, neither precision nor counting, nor their interaction, affected acceleration time (all F s < 1.78). However, precision affected both deceleration time, $F [1,14] = 24.61, p < 0.001, \eta^2 = .63$, and the number of online adjustments, $F [1,14] = 54.46, p < 0.05, \eta^2 = .77$. Participants spent more time in deceleration, and had a greater number of online adjustments, in the high precision than the low precision condition. Neither counting, nor its interactions with precision, affected deceleration time or online adjustments (all F s < 2.4).

For the tossing/placing portion of the movement, both precision, $F [1,14] = 84.67, p < 0.001, \eta^2 = .72$, and counting, $F [1,14] = 9.71, p < 0.01, \eta^2 = .12$, affected time spent in acceleration, as did their interaction, $F [1,14] = 6.34, p < 0.05, \eta^2 = .05$. Participants spent more time in the acceleration phase of the movement in the high precision vs. low precision condition, and also in the counting condition vs. no counting, and these effects were additive. More importantly, and again consistent with precision affecting online control, there were even greater effects of precision on time spent in deceleration, $F [1,14] = 401.92, p < 0.001, \eta^2 = .94$. Counting also affected time spent in deceleration, $F [1,14] = 10.22, p < 0.01, \eta^2 = .03$, but the interaction was not significant, $F [1, 14] = 1.24, p > 0.10$. Finally, although the number of online adjustments was greater in the high precision than low precision condition, $F [1,14] = 256.46, p < 0.001, \eta^2 = .91$, there was no effect of counting, nor its interaction with precision, on online adjustments (both F s < 2.44).

Discussion

Experiment 2 examined the effects of an interference task on motor imagery and overt action. The Motor-Cognitive Model predicted that, as the elaboration of motor imagery relies on a conscious process utilizing executive resources, simultaneously taxing these resources with the backwards counting task would interfere with the ability to elaborate the image and/or to switch attention between the image and the indexing response. In both steps of the placing/tossing task, this was what occurred: participants were much slower in performing the motor imagery task during the counting condition than during the no counting condition, whereas the effects of the counting task on overt action were minimal.

The Functional Equivalence Model, in comparison, holds that motor imagery and overt action operate using the same internal representations. Thus, a secondary task that interferes with one behaviour should interfere with the other to a comparable extent.

Although the counting task did have some effect on overt actions (increasing the time spent in deceleration), its overall effect was not comparable to its effect on motor imagery. Nevertheless, we would caution against generalising our findings on interference effects to longer-lasting, more complex actions. Indeed, some action sequences such as locomotion can be susceptible to interference from secondary cognitive tasks, including backwards counting (Abdolvahab, 2015; Yardley & Higgins, 1998).

As had occurred in Experiment 1b, participants in the motor imagery conditions had longer movement times than those performing the overt actions, even in the low-precision conditions. In the no counting/low-precision combination in particular, there was no theoretical reason to think that motor imagery should have longer movement times than overt actions. However, as in Experiment 1b, we note that the keyboard may have acted an obstacle to participants in the motor imagery condition. Further, a potential confound in all the previous experiments was that there were no indexing requirements for the overt action version of the task. Thus, a proponent of the Functional Equivalence Model could argue that the two tasks were not matched. Indeed, one could argue that the longer movement times in the high precision and counting conditions of the motor imagery condition resulted from the need to perform the extra indexing response simultaneously with the imagery.

In order to address these possible confounds, we ran a control experiment in which the two tasks were closely matched. In Experiment 3, participants in the overt action condition had to index the timing of their responses on the keyboard while they reached to grasp and toss/place the object. We included the counting/no-counting conditions as well, as these had the largest effects on motor imagery. This setup thus allowed us to match the overt action and motor imagery tasks for both the presence of the keyboard and the requirement to perform the indexing response, as well as how these might interact with the counting task.

Experiment 3

Experiment 3 was set up to test whether having the keyboard present and performing the indexing response during overt actions would have a similar impact on their timing as they did on motor imagery. The Motor Cognitive Model would predict that the keyboard and the secondary task of pressing the key during performance of the overt action should not alter the main results of Experiment 2. Specifically, both precision and counting should have greater effects on the timing of motor imagery than overt actions. Conversely, a proponent of the Functional Equivalence Model would argue that any differences observed previously between the timing of overt actions and motor imagery should be eliminated once the tasks

are fully matched. On this account, there should be no effect of group (overt action vs. motor imagery), nor any interactions between group and other variables, in the present experiment.

Methods

Participants

A new set of 32 undergraduates at Royal Holloway University of London took part in Experiment 3 in return for course credit. As before, half were randomly assigned to the motor imagery condition, and half to the overt action condition. Participants completed the experiment in a single session lasting approximately 20 minutes. There were seven males and twenty-five females (mean age 19 years). All participants had normal or corrected vision, were right-handed by self-report, and had no motor or neurological impairments. All gave informed consent prior to testing, and all were naïve as to the exact purpose of the study. The experimental protocol was approved by the Psychology Departmental Ethics Committee at Royal Holloway University of London.

Stimuli and Apparatus

Experiment 3 used the same apparatus for both the motor imagery and overt action conditions (Figure 1, top right panel).

Procedure

The order of trial presentation followed the same ABBA pattern as in Experiment 2. In the motor imagery condition, the procedure was identical to that of Experiment 2. In the overt action condition, the procedure was identical in terms of the requirement to reach-to-grasp the disc and then either toss it into the box (low precision) or place it into the cylinder (high precision) using the right hand. Unlike Experiment 2, participants in the overt action condition were also required to reach over the keyboard to execute the movement, just as participants had to imagine reaching over it in the motor imagery condition. Further, participants in the overt action condition were instructed to rest their left index finger on the 'd' key, and to press it three times coincident with 1) the initiation of the movement; 2) the initial grasp of the disc; and 3) the completion of the tossing/placing portion of the action. The timing of these presses corresponded to their timings for participants in the motor imagery condition. The experimenter monitored the participants in the overt action group to ensure they pressed the button at the appropriate times; failure to do so led to the trial being repeated.

Design and Analysis

Movement times for both the overt action and motor imagery groups were indexed as the timing of the second and third button presses, corresponding to the indexing of movement times in the motor imagery condition in Experiments 1b and 2. As in Experiment 2, group (overt action vs. motor imagery) was a between-subjects variable, whereas precision and counting were within-subjects variables. The result was two 2x2x2 mixed ANOVAs, one for each stage of the movement. No kinematics were recorded, as pilot testing showed that the electronics in the keyboard unfortunately disrupted the measurements of the Polhemus movement recording system.

Results

Overall, the results replicated the main results of Experiment 2, again supporting the Motor-Cognitive Model over the Functional Equivalence Model. The first ANOVA examined the initial reach-to-grasp movement of the disc (Figure 6). As in Experiment 2, there were longer movement times in the motor imagery vs. overt action condition, $F [1, 30] = 11.63, p < 0.01, \eta^2 = .28$, in the high precision vs. low precision condition, $F [1, 30] = 16.72, p < 0.001, \eta^2 = .36$, and in the counting vs. no counting condition, $F [1, 15] = 15.49, p < 0.001, \eta^2 = .34$. The interaction between precision and counting was not significant, $F [1, 15] = 2.49, p > 0.10$.

Most importantly, and as predicted by the Motor-Cognitive Model but not the Functional Equivalence Model, there was again a significant interaction between group and counting, $F [1, 30] = 8.07, p < 0.01, \eta^2 = .21$, with counting having a much larger effect on motor imagery than on overt action. Also consistent with the Motor-Cognitive Model, there was again a significant interaction between group and precision, $F [1, 30] = 4.71, p < 0.05, \eta^2 = .14$, with precision affecting motor imagery more than overt action. Finally, although there was a tendency for the effects of counting and precision on group to be additive, there was no evidence for a three-way interaction, $F [1, 15] = 1.32, p > 0.10$.

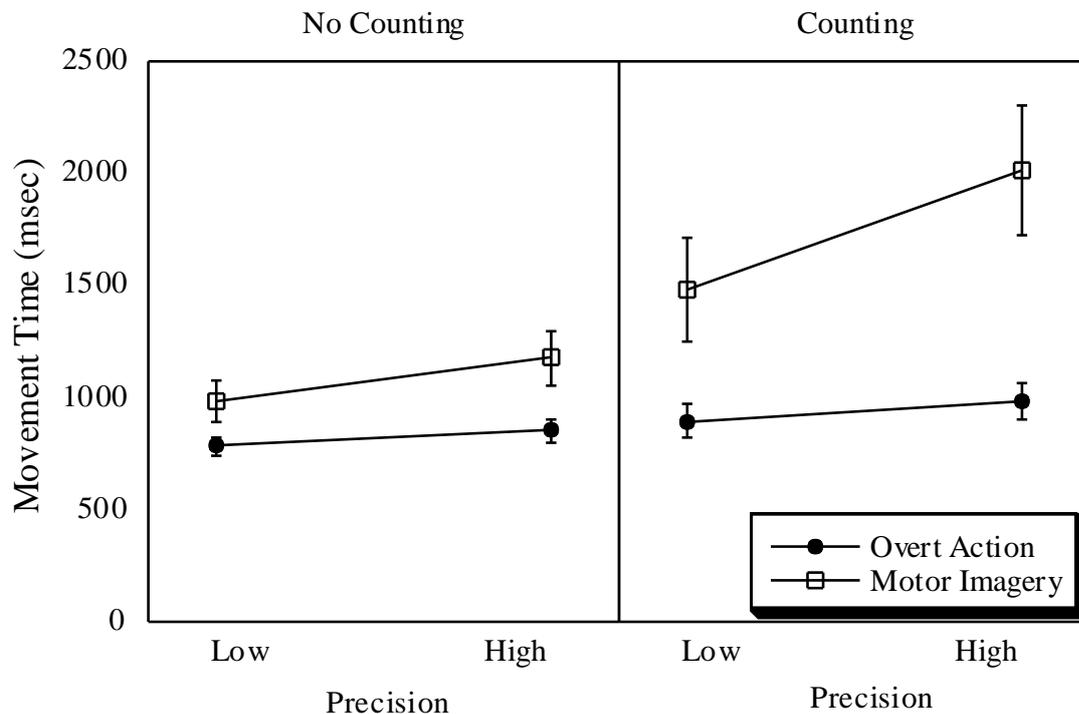


Figure 6. Effect of precision and counting on imagined and overt movement times in the initial reach-to-grasp of the disc in Experiment 3. Left: No counting condition. Right: Counting condition. Error bars represent standard errors of the mean.

The second ANOVA examined movement times in the tossing/placing portion of the movement (Figure 7), and again broadly matched the results of Experiment 2. Movement times were longer in the motor imagery vs. overt action condition, $F [1, 15] = 22.70, p < 0.001, \eta^2 = .43$, in the high precision vs. low precision condition, $F [1, 15] = 31.82, p < 0.001, \eta^2 = .52$, and in the counting vs. no counting conditions, $F [1, 15] = 14.04, p < 0.01, \eta^2 = .32$. There was no evidence that counting interacted with precision, $F [1, 15] = 0.49, p > 0.10, \eta^2 = .02$.

As in Experiment 2, the critical interaction between the group and counting/nocounting was significant, $F [1, 15] = 6.43, p < 0.05, \eta^2 = .18$, with counting affecting motor imagery more than overt action. The predicted interaction between group and precision was also present, $F [1, 15] = 14.70, p < 0.01, \eta^2 = .33$, with the effect of increasing precision being greater on motor imagery than on overt action. Finally, the three way

interaction between group, precision, and counting was not significant, $F [1, 14] = 1.24, p > 0.10$.

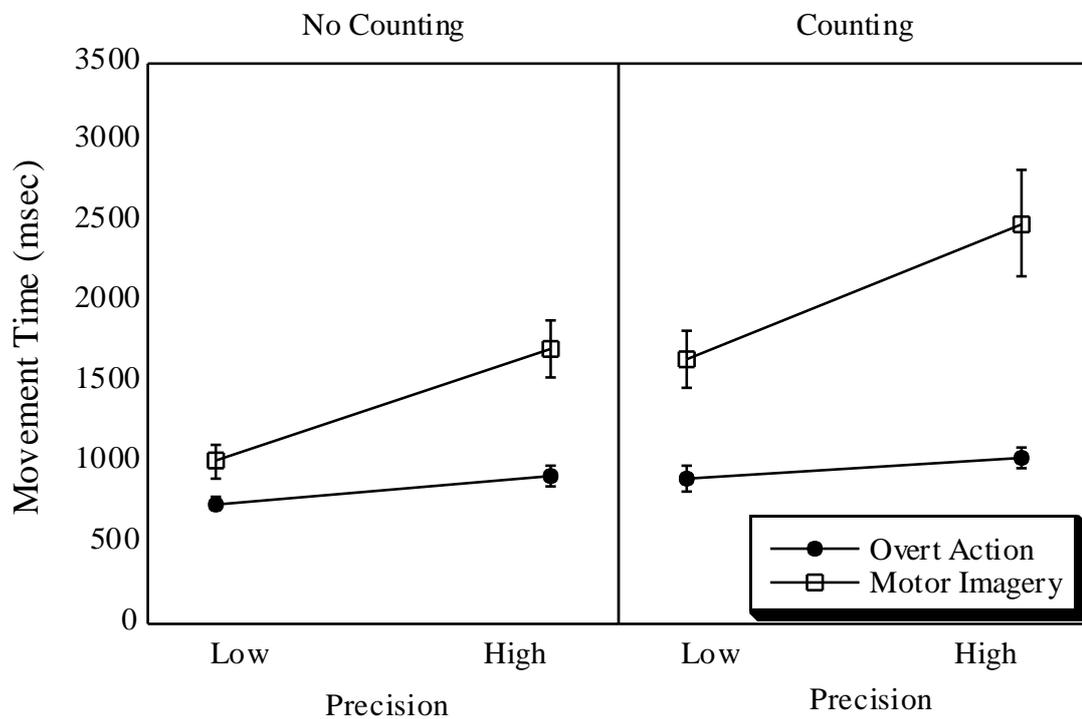


Figure 7. Comparison of precision and counting effects on imagined and overt movement times in the second phase of the movement in Experiment 3 (low-precision tossing versus high-precision placing). Error bars represent standard errors of the mean.

Discussion

Matching the motor imagery and overt action tasks, including both the presence of the keyboard and the requirement to index the movements with button presses, did not alter the main results of the previous experiment. Again, there was clear evidence that motor imagery was more affected by both precision and counting than was overt action, as predicted by the Motor Cognitive Model but not the Functional Equivalence Model.

Interestingly, despite having matched the tasks more closely, motor imagery continued to take longer than overt actions overall, even in the no-counting condition. Previously we suggested this might be a consequence of the keyboard serving as an obstacle.

However, this cannot be the case as here the keyboard was also present in the overt action condition. Moreover, there was no indication that participants failed to faithfully time the execution of the indexing task in the overt action condition. In fact the means in the overt action conditions were slightly longer than in Experiment 2, as one might expect when they had to reach over and around an obstacle. It's unclear at present why this result occurs so consistently in this task but was not evident in the egg lifting task used in Experiment 1a. One possibility is that the effect may be present in both tasks, but simply was not detected in Experiment 1a.

Finally, we note that some effects found in Experiment 2 did not reproduce here, i.e., there was an absence of the interactions between counting and precision as had occurred in Experiment 2. There was also no three way interaction between counting, precision, and group as had occurred in the second stage of the movement of Experiment 2. However, we contend that none of these interactions would have been predicted by either model *a priori*, and thus whether or not they ultimately prove to be robust is of lesser theoretical import. It is possible the effects of precision and counting either are additive or are not additive, for example, with either outcome being consistent with the Motor-Cognitive Model. Additive effects may reflect an overall increased use of central executive resources, whereas nonadditive effects may reflect the use of different types of executive resources in elaborating the motor image and switching between the image and the indexing response. In other words, both the counting and key pressing may interfere with motor imagery, but not with each other. Anecdotal evidence for this notion was that many participants in the motor imagery group had a spontaneous tendency to press the button at the same time as verbalizing the next number in the sequence (this tendency was not evident in participants in the overt action group). When queried about this, they typically remarked that they had to switch back-and-forth between imagining the movements and doing the other two tasks.

General Discussion

We here outlined the Motor Cognitive Model of motor imagery and tested its predictions against those of the Functional Equivalence Model. In several experiments, we showed that motor imagery can be functionally dissociated from overt actions. When precision was manipulated, it was found to have greater effects on imagined than on overt movement times. These results were consistent with the tenet of the Motor-Cognitive Model that motor imagery should be impaired at simulating movement times when the actions

themselves rely more on online control, owing to lower fidelity motor representations, a greater need to consciously generate images, and a concomitant delay in the switching of attention between the motor image and the indexing response.

In Experiment 2, participants were also required to perform a backwards counting task while simultaneously performing the task using either motor imagery or overt action. Here, motor imagery was slowed greatly by the inclusion of the interference task, whereas its effects on the timing of overt action were minimal. This result was also consistent with the Motor-Cognitive Model, which holds that executive resources are needed to elaborate the motor image during its execution, and to switch attention between the image and its indexing response. Overloading these resources resulted in large increases in imagined movement times. Experiment 3 showed that the results of the other experiments could not be due to inadequate matching between the overt action and motor imagery tasks. Including the keyboard and the requirement to index the timing of the response in the overt action version of the task did not eliminate the greater effects of precision and counting on motor imagery compared to overt actions.

None of the experiments here can be easily reconciled with the Functional Equivalence Model. According to this view, motor imagery utilizes the same internal processes as real actions. As such, motor imagery should closely mirror the time required to execute overt actions under all types of conditions, with both imagery and overt action being similarly affected by different variables and secondary tasks. This model would not have predicted the effects of the precision and interference manipulations we found here.

Adapting the Functional Equivalence Model

Although a strong version of the Functional Equivalence Model was not supported by the present study, there are weakened variants of this model that might attempt to explain our findings. For example, Decety et al. (1989) used the representation of force as an explanation for overestimations by motor imagery caused by carrying an external load. Participants in their study either walked, or imagined walking, a distance of 5, 10 or 15 metres, either unencumbered or while carrying a 25kg load. Whereas participants in the no load condition matched their real and imagined movement times, participants in the load condition overestimated the time required to walk the distance using motor imagery. Similar results have been reported using external loads during manual actions (Macuga et al., 2012; Slifkin, 2008).

Decety et al. explained their finding as resulting from motor imagery using an estimate of the force required to carry the extra load to estimate imagined movement times. According to this variant of the Functional Equivalence Model, under some circumstances motor imagery uses a representation of the force required by the movement rather than a representation of the movement's timing.

Even this weakened version of the Functional Equivalence Model would have difficulty explaining the results of the present study, however. For example, it seems unlikely that the high precision variants of the tasks used in Experiments 1a and 1b required more force to execute than did their low precision counterparts, as both movements covered the same distance and involved targets of identical weights. Beyond this, there is certainly no reason to think that the movements made in Experiments 2 and 3 required more force when participants counted backwards than when they did not.

One might adapt the Functional Equivalence Model further by arguing that instead of using the representation of force, motor imagery sometimes uses a representation of perceived effort to simulate movement times. On this account, the movements in the high precision conditions of Experiments 1a and 1b, which were more difficult to execute than their low precision counterparts, would have resulted in longer movement times during motor imagery than overt actions. However, this further adaptation of the model still fails to explain the large discrepancy between overt and imagined movement times in the counting conditions of Experiments 2 and 3, as participants showed much smaller effects of the counting task on overt actions. Although it's possible that the counting version of the overt action task may have been perceived as involving more effort than the non-counting version, it did not slow down the overt actions anywhere nearly as much as it slowed down motor imagery. Overall then, it is hard to reconcile even these weakened versions of the Functional Equivalence Model with the results of the three experiments reported here.

Planning and Control in Motor Imagery

The planning-control distinction in overt action is well-established (Elliott et al., 2001; Glover, 2004; Glover & Dixon, 2001; Woodworth, 1899), with numerous variables being shown to affect one of these stages of action but not the other (Glover & Dixon, 2001, 2002; Glover et al., 2004). For example, visual illusions and word labels both can affect movement planning, whereas neither affects online control (Glover & Dixon, 2001; 2002a, 2002b). Further, online control has been shown to be a much faster process than movement planning (Paulignan et al., 1991; Zelaznik, Hawkins, & Kisselburgh, 1983), and one that

occurs outside of conscious awareness (Goodale et al., 1992; Pisella et al., 2000).

Despite the clear differences between planning and control however, the importance of this distinction to motor imagery has previously received little attention. This is somewhat surprising because in the absence of an online control phase, it is difficult to conceive of how motor imagery can truly be functionally equivalent to overt action. Clearly there are numerous situations in which overt actions rely heavily on online control and which it would be difficult if not impossible to faithfully simulate using a motor imagery process reliant entirely on internal motor representations. One example of this would be a task in which a target's location was suddenly perturbed after movement initiation (Castiello, Bennett, & Chambers, 1998; Goodale, et al., 1992). In this kind of task, motor imagery would presumably be unable to simulate the fast and automatic responses to the perturbation that occur during overt action (Goodale et al., 1992; Paulignan et al., 1991; Pisella et al., 2000), but would rather require a conscious intervention acting on the motor image to adjust the originally intended (simulated) movement. This might result in a greater number of errors being reported when imagining a movement involving a target perturbation than when overtly responding to it, or a relative lengthening of simulated movement times in perturbation conditions, similar to the effects observed in overt actions for patients with damage to the online control system (Pisella et al., 2000). Further, given the results of the present study, the conscious adjustments of movement simulation required for motor imagery should also be susceptible to interference from a concurrent task to a much greater extent than the automatic and unconscious adjustments made during overt action.

The distinction between planning and control also exists neurologically (Glover, 2004; Glover, Wall, & Smith, 2012). Thus, one should expect to find more neurological similarities between motor imagery and action planning than between motor imagery and online control (Glover, 2004). An fMRI study by Macuga and Frey (2014) supported this hypothesis in its comparison of the neural activity during motor imagery versus open-loop and closed-loop aiming. The key result for the Motor-Cognitive Model was that activity in dorsolateral prefrontal and inferior frontal regions was greatest when using motor imagery, but was also greater when movements were carried out under visual open-loop compared to closed-loop. The implication of this finding is that these brain regions may also be used to consciously elaborate overt actions carried out when online feedback is degraded or absent. If this is true, one might logically expect to find larger effects of an interference task on an open-loop action than the minimal effects observed here when the action was closed-loop.

Limitations of the Motor-Cognitive Model

Although the Motor-Cognitive Model outperforms the Functional Equivalence Model in predicting and explaining the results of the present study and many others (e.g., Calmels & Fournier, 2001; Calmels et al., 2006; Cerritelli et al., 2000; Chandrasekharan et al., 2012; Cohen et al., 2011; Decety et al., 1989; Filimon et al., 2007; Guillot et al., 2009; Macuga & Frey 2014; Olsson & Nyberg, 2011; Yoxon et al., 2015), there also exist findings that suggest it requires further testing and refinement. For example, Rieger (2012) examined the effects of expertise on touch vs. hunt-and-peck typists. Both pairs were asked to imagine typing a set of text using either their preferred method or their non-preferred method. Here, the Motor Cognitive Model would predict that participants should take longer to imagine the movements using their non-preferred method than to execute them. Instead, hunt-and-peck typists actually took less time to imagine than execute movements using either method whereas touch typists generally matched motor imagery and overt action times using both methods. One possible explanation for this is that the touch typists may in fact have better developed representations of hunt-and-peck typing than the hunt-and-peck typists have of touch typing, allowing the former group to simulate more precisely the timing of either method. Further systematic testing of the effects of expertise on motor imagery could help to clarify this question.

Other results suggest that longer-lasting movements are more likely to have imagined movement times that are shorter than the corresponding overt times, as compared to shorter duration movements in which motor imagery is more likely to take longer than overt actions (e.g., Kunz, Creem-Regehr, & Thompson, 2009; Rieger & Massen, 2014; Rodriguez, Llanos, Gonzalez, & Sabate, 2008; see Guillot et al., 2012, for a review). A reason for this may be that movement times longer than a few seconds are too long for the relatively short-lived costs of switching attention on executive function to be evident. In these cases, the timing of motor imagery may be more influenced by factors other than the fidelity of the image, although it is unclear at present what exactly these factors might be. At this point, the pattern of results in the literature suggests that the Motor Cognitive Model as it currently stands may be most applicable to movements lasting less than a few seconds.

Other aspects of the Motor-Cognitive Model may also require elaboration: For example, whereas it provides a reasonable account of how motor imagery deals with the absence of online feedback during execution, it as yet does not attempt to explain how the lack of knowledge of results may impact motor imagery. In overt actions, knowing the consequences of an action allows one to calibrate future movements to improve accuracy

(Fajen, 2005; Kunz et al., 2009). Without this information, motor imagery should not benefit from practice to the same extent as overt actions – this may explain why motor imagery times are generally much more variable than overt action times (Papaxanthis et al. 2002; Rieger, 2012).

Finally, the Motor Cognitive framework at this stage provides no accounting of the role of forward models Grush (2004; cf. Wolpert & Ghahramani, 2000), whereas it has been argued by Grush (2004) that such forward models must play a vital role in motor imagery. Thus, a future version of the Motor Cognitive Model may need to elaborate on the role, if any, forward modelling may have in motor imagery. Taking all of these factors in sum, it seems apt to conclude that at this stage the Motor Cognitive Model requires further testing and refinement in order to more fully accommodate the vast breadth of studies on motor imagery.

Imagery vs. Overt Sensation in Perception and Action

A comparison of perceptual imagery to overt sensation may be informative in understanding the distinction between motor imagery and overt action. Early theories of visual imagery took a comparable approach to the Functional Equivalence Model, emphasizing the similarities between visual imagery and perception (Kosslyn, 1980). However, more detailed examination has since catalogued a number of key differences between visual imagery and visual perception. For example, visual images are less effective primes than are overt percepts (McDermott & Roediger, 1994; Michelson & Zacks, 2003); visual images are often not amenable to perceptual switching between interpretations (Chambers & Reisberg, 1985); images and percepts have different directional flows of brain activation (Dentico et al., 2014); and neuropsychological dissociations exist between deficits in imagery and deficits in perception (Behrmann, Moscovitch, & Winocur, 1994; Farah, 1984; Guariglia, Padovani, Pantano, & Pizzamiglio, 1993). More recent models of visual imagery have acknowledged these differences by arguing that although both imagery and perception activate the same sensory buffer, imagery does so in a top-down fashion whereas perception does so in a bottom-up fashion (Kosslyn, 1994).

What comparisons can be drawn between motor and perceptual imagery? Both involve the use of top-down stored representations, and both lack bottom-up sensory input. We suggest that these facts may have different consequences depending on the type of imagery. In the case of perceptual imagery, it is the means by which images are initially generated that must occur in a top-down fashion, whereas their execution can be maintained

using internal representations. In contrast, a motor image can initially be generated using internal representations, but the elaboration and monitoring of the image requires top-down processes. Common to both sensory and motor imagery, neither can adequately be explained by a simple one-to-one functional and neurological mapping with its overt counterpart. Like perceptual imagery then, we suggest that understanding motor imagery requires an accounting of both its differences as well as its similarities with overt actions.

Conclusions

The Motor-Cognitive Model posits a role of executive functions in motor imagery that is not evident in overt actions. As a consequence, motor imagery can be functionally dissociable from overt actions under conditions which emphasize executive functions. Such conditions include when the internal representations of an action have a low fidelity with the motor output, or when attention is shared between motor imagery and other cognitive tasks. This is in contrast to the tenets of the Functional Equivalence Model, which argues that motor imagery should have nearly identical outputs to overt actions under nearly all circumstances. A review of the extant literature showed that only the Motor-Cognitive Model could predict and explain many of the behavioral and neurological differences between motor imagery and overt actions. In testing the models directly, we observed several results consistent with the Motor-Cognitive Model but not the Functional Equivalence Model. We conclude that the Motor-Cognitive Model thus represents a promising first step towards a comprehensive theory of motor imagery.

References

- Abdolvahab, M. (2015). Gait transition dynamics are modulated by concurrent cognitive activity. *Attention, Perception, and Psychophysics*, *77*, 2502-2506.
- Aflalo, T., Kellis, S., Klaes, C., Lee, B., Shi, Y., Pejsa, K., Shanfield, K., Hayes-Jackson, S., Aisen, M., Heck, C., Liu, C., & Andersen, R. A. (2015). Neurophysiology. Decoding motor imagery from the posterior parietal cortex of a tetraplegic human. *Science*, *348*, 906-910.
- Bennabi, D., Monnin, J., Haffen, E., Carvalho, N., Vandell, P., Pozzo, T., & Papaxanthis, C. (2014). Motor imagery in unipolar major depression. *Frontiers in Behavioral Neuroscience*. doi: 10.3389/fmbeh.2014.00413.
- Behrmann, M., Moscovitch, M., & Winocur, G. (1994). Intact visual imagery and impaired visual perception in a patient with visual agnosia. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 1068-1087.
- Blair, A., Hall, C., & Leyshon, G. (1993). Imagery effects on the performance of skilled and novice soccer players. *Journal of Sports Science*, *11*, 95-101.
- Calmels, C., & Fournier, J. F. (2001). Duration of physical and mental execution of gymnastic routines. *The Sport Psychologist*, *15*, 142-150.
- Calmels, C., Holmes, P., Lopez, E., & Naman, V. (2006). Chronometric comparison of actual and imagined complex movement patterns. *Journal of Motor Behavior*, *38*, 339-348.
- Cameron, B. D., Enns, J. T., Franks, I. M., & Chua, R. (2009). The hand's automatic pilot can update visual information while the eye is in motion. *Experimental Brain Research*, *195*, 445-454.
- Castiello, U., Bennett, K., & Stelmach, G. (1993). Reach to grasp: the natural response to perturbation of object size. *Experimental Brain Research*, *94*, 163-178.
- Cerritelli, B., Maruff, P., Wilson, P. H., & Currie, J. (2000). The effect of an external load on the force and timing of mentally represented actions. *Behavioural Brain Research*, *77*, 45-52.

- Chandrasekharan, S., Binsted, g., Ayres, F., Higgins, L., & Welsh, T. N. (2012). Factors that affect action possibility judgments: recent experience with the action and the current body state. *Quarterly Journal of Experimental Psychology*, *65*, 976.
- Chambers, D., & Reisberg, D. (1992). What an image depicts depends on what an image means. *Cognitive Psychology*, *24*, 145-170.
- Cohen, R. G., Chao, A., Nutt, J. G., & Horak, F. B. (2009). Freezing of gait is associated with a mismatch between motor imagery and motor execution in narrow doorways, not with failure to judge doorway passability. *Neuropsychologia*, *40*, 3081-3088.
- Danckert, J., Ferber, S., Doherty, T., Steinmetz, H., Nicolle, D., & Goodale, M. A. (2002). Selective, non-lateralized impairment of motor imagery following right parietal damage. *Neurocase*, *8*, 194-204.
- Decety, J. (1996). Neural representations for action. *Reviews in the Neurosciences*, *7*, 285-297.
- Decety, J., & Jeannerod, M. (1995). Mentally simulated movements in virtual reality: does Fitts' Law hold in motor imagery? *Behavioural Brain Research*, *72*, 127-134.
- Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented action. *Behavioural Brain Research*, *34*, 35-42.
- Decety, J., & Michel, F. (1989). Comparative analysis of actual and mental movement times in two graphic tasks. *Brain and Cognition*, *11*, 87-97.
- Denis, M. (1985). Visual imagery and the use of mental practice in the development of motor skills. *Canadian Journal of Applied Sports Science*, *10*, 4S-16S.
- Dentico, D., Cheung, B. L., Chang, J-Y., Guokas, J., Boly, M., Tononi, G., & Van Veen, B. (2014). Reversal of cortical information flow during visual imagery as compared to visual perception. *Neuroimage*, *100*, 237-243.
- Dietrich, A. (2008). Imagining the imagination: the trouble with motor imagery. *Methods*, *45*, 319-324.

- Dux, P. E., Tombu, M. N., Harrison, S., Rogers, B. P., Tong, F., & Marois, R. (2009). Training improves multitasking performance by increasing the speed of information processing in human prefrontal cortex. *Neuron*, *63*, 127-138.
- Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two component model of goal-directed aiming. *Psychological Bulletin*, *127*, 342-357.
- Farah, M. J. (1984). The neurological basis of mental imagery: A componential analysis. *Cognition*, *18*, 245-272.
- Fikes, T. G., Klatzky, R., & Lederman, S. (1994). Effects of object texture on precontact movement time in human prehension. *Journal of Motor Behavior*, *26*, 325-332.
- Filimon, F., Nelson, J., Hagler, D., & Sereno, M. (2007). Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *NeuroImage*, *37*, 1315-1328.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, *47*, 381-391.
- Gandrey, P., Paizis, C., Karathanasis, V., Gueugneau, N., & Papaxanthis, C. (2013). Dominant vs. nondominant arm advantage in mentally simulated actions in right handers. *Journal of Neurophysiology*, *110*, 2887-2894.
- Gentilucci, M., Negrotti, A., & Gangitano, M. (1997). Planning an action. *Experimental Brain Research*, *115*, 116-128.
- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., Agid, Y., & Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*, *10*, 1093-1104.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, *27*, 3-24.
- Glover, S., & Dixon, P. (2001). Dynamic illusion effects in a reaching task: evidence for separate visual representations in the planning and control of action. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 560-572.

- Glover, S., & Dixon, P. (2002a). Dynamic effects of the Ebbinghaus illusion in grasping: support for a planning/control model of action. *Perception and Psychophysics*, 64, 266-278.
- Glover, S., & Dixon, P. (2002b). Semantics affect the planning but not control of grasping. *Experimental Brain Research*, 146, 383-387.
- Glover, S., & Dixon, P. (2013). Context and vision effects on real and imagined actions: support for the common representation hypothesis of motor imagery. *Journal of Experimental Psychology: Human Perception and Performance*.
- Glover, S., Dixon, P., Castiello, U., & Rushworth, M. F. (2005). Effects of an orientation illusion on motor performance and motor imagery. *Experimental Brain Research*, 166, 17-22.
- Glover, S., Rosenbaum, D. A., Graham, J. R., & Dixon, P. (2004). Grasping the meaning of words. *Experimental Brain Research*, 154, 383-387.
- Glover, S., Wall, M. B., & Smith, A. T. (2012). Distinct cortical regions support the planning and on-line control of reaching-to-grasp in humans. *European Journal of Neuroscience*, 35, 909-915.
- Goodale, M. A., Pelisson, D., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, 320, 748-750.
- Grabherr, L., Jola, C., Berra, G., Theiler, R., & Mast, F. W. (2015). Motor imagery training improves precision of an upper limb movement in patients with hemiparesis. *NeuroRehabilitation*, in press.
- Grealy, M. A., & Lee, D. N. (2011). An automatic-voluntary dissociation and mental imagery disturbance following a cerebellar lesion. *Neuropsychologia*, 49, 271-275.
- Grealy, M. A., & Shearer, G. F. (2006). Timing processes in motor imagery. *European Journal of Cognitive Psychology*, 20, 867-892.
- Grush, R. (2004). The emulation theory of representation: motor control, imagery, and perception. *Behavioral and Brain Sciences*, 27, 377-396.

- Guariglia, C., Padovani, A., Pantano, P., & Pizzamiglio, L. (1993). Unilateral neglect restricted to visual imagery. *Nature*, *364*, 235-237.
- Guillot, A., & Collet, C. (2005). Contribution from neurophysiological and psychological methods to the study of motor imagery. *Brain Research Reviews*, *50*, 387-397.
- Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2009). Brain activity during visual versus kinesthetic imagery: an fMRI study. *Human Brain Mapping*, *30*, 2157-2172.
- Guillot, A., Hoyek, N., Louis, M., & Collet, C. (2012). Understanding the timing of motor imagery: recent findings and future directions. *International Review of Sport and Exercise Psychology*, *5*, 3-22.
- Hanyu, K., & Itsukushima, Y. (2000). Cognitive distance of stairways: A multi-stairway investigation. *Scandinavian Journal of Psychology*, *41*, 63-69.
- Harris, J., & Hebert, A. (2015). Utilization of motor imagery in upper limb rehabilitation: A systematic scoping review. *Clinical Rehabilitation*, in press.
- Hetu, S., Gregoire, M., Saimpont, A., Coll, M.-P., Eugene, F., Michon, P.-E., & Jackson, P. (2013). The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and Biobehavioral Reviews*, *37*, 930-949.
- Hummelsheim, H. (1999). Rationales for improving motor function. *Current Opinion Neurology*, *12*, 697-701.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*, 187-245.
- Jeannerod, M. (2001). Neural simulation of action: a unifying mechanism for motor cognition. *Neuroimage*, *14*, S103-109.
- Jiang, D., Edwards, M. G., Mullins, P., & Callow, N. (2015). The neural substrates for the different modalities of movement imagery. *Brain and Cognition*, *97*, 22-31.

- Kosslyn, S. M. (1980). *Image and mind*. Cambridge, MA: Harvard University Press.
- Kosslyn, S. M. (1994). *Image and brain*. Cambridge, MA: Harvard University Press.
- Kunz, B. R., Creem-Regehr, S. H., & Thompson, W. B. (2009). Evidence for motor simulation in imagined locomotion. *Journal of Experimental Psychology: Human Perception and Performance*, *35*, 1458-1471.
- MacIntyre, T., & Moran, A. (1996). Imagery validation: how do we know athletes are imagining during mental practice. *Journal of Applied Sport Psychology*, *8*, 132.
- Macuga, K. L., & Frey, S. H. (2012). Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage*, *59*, 2798-2807.
- Macuga, K. L., & Frey, S. H. (2014). Differential contributions of the superior and inferior parietal cortex to feedback versus feedforward control of tools. *Neuroimage*, *92*, 36-52.
- Macuga, K. L., Papailiou, A. P., & Frey, S. H. (2012). Motor imagery of tool use: relationship to actual use and adherence to Fitts' law across tasks. *Experimental Brain Research*, *218*, 11.
- Marteniuk, R. G., MacKenzie, C. L., Jeannerod, M., Athenes, S., & Dugas, C. (1987). Constraints on human arm movement trajectories. *Canadian Journal of Psychology*, *41*, 365-378.
- Maruff, P., Wilson, P. H., De Fazio, J., Cerritelli, B., Hedt, A., & Currie, J. (1999). Asymmetries between dominant and non-dominant hands in real and imagined motor task performance. *Neuropsychologia*, *37*, 379-384.
- McDermott, K. B., & Roediger, H. L. (1994). Effects of imagery on perceptual implicit memory tests. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 1379-1390.
- McInnes, K., Friesen, C., & Boe, S. (2016). Specific brain lesions impair explicit motor imagery ability: a systematic review of the evidence. *Archives in Physiology, Medicine, & Rehabilitation*, *97*, 478-489.

- Meyer, D. E., Abrams, R. A., Kornblum, S., Wright, C. E., & Smith, K. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, *95*, 340-370.
- Michelson, P., & Zacks, J. M. (2003). What is primed in priming from imagery? *Psychological Research*, *67*, 71-79.
- Miller, K. J., Schalk, G., Fetz, E. E., den Njis, M., Ojermann, J., & Rao, R. P. (2010). Cortical activity during motor execution, motor imagery, and motor imagery-based online feedback. *PNAS Proceedings of the National Academy of Sciences of the USA*, *107*, 4430-4435.
- Moran, A., Guillot, A., Macintyre, T., & Collet, C. (2012). Re-imagining motor imagery: building bridges between cognitive neuroscience and sport psychology. *British Journal of Psychology*, *103*, 224-247.
- Nair, D. G., Purcott, K. L., Fuchs, A., Steinberg, F., & Kelso, J. A. (2003). Cortical and cerebellar activity of the human brain during imagined and executed unimanual and bimanual action sequences: a functional MRI study. *Brain Research Cognitive Brain Research*, *15*, 250-260.
- Nieuwenstein, M., & Wyble, B. (2014). Beyond a mask and against the bottleneck: retroactive dual-task interference during working memory consolidation of a masked visual target. *Journal of Experimental Psychology: General*, *143*, 1409-1427.
- Oishi, T., Kasai, T., & Maeshima, T. (2000). Autonomic response specificity during motor imagery. *Journal of Physiology, Anthropology, and Applied Human Science*, *19*, 255-261.
- Olsson, C. J., & Nyberg, L. (2011). Brain simulation of action may be grounded in physical experience. *Neurocase*, *17*, 501-505.
- Papaxanthis, C., Pozzo, T., Skoura, X., & Schieppati, M. (2002). Does order and timing in performance of imagined and actual movements affect the motor imagery process? The duration of walking and writing tasks. *Behavioural Brain Research*, *134*, 209-215.

- Paulignan, Y., MacKenzie, C. L., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements. I. The effects of changing object position. *Experimental Brain Research*, *83*, 505-512.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An “automatic pilot” for the hand in human posterior parietal cortex: towards reinterpreting optic ataxia. *Nature Neuroscience*, *3*, 729-736.
- Pylyshyn, Z. W. (2002). Mental imagery: in search of a theory. *Behavioral and Brain Sciences*, *25*, 157-182.
- Rademaker, R. L., Bloem, I. M., De Weerd, P., & Sack, A. T. (2015). The impact of interference on short-term memory for visual orientation. *Journal of Experimental Psychology: Human Perception and Performance*, in press.
- Rieger, M. (2012). Motor imagery in typing: effects of typing style and action familiarity. *Psychonomic Bulletin and Review*, *19*, 101-107.
- Rieger, M., & Massen, C. (2014). Tool characteristics in imagery of tool actions. *Psychological Research*, *78*, 10-17.
- Rodriguez, M., Llanos, C., Gonzalez, S., & Sabate, M. (2008). How similar are motor imagery and movement. *Behavioral Neuroscience*, *122*, 910-916.
- Rodriguez, M., Llanos, C., & Sabate, M. (2009). The kinematics of motor imagery: Comparing the dynamics of real and virtual movements. *Neuropsychologia*, *47*, 489-496.
- Saimpont, A., Malouin, F., Tousignant, B., & Jackson, P. L. (2012). The influence of body configuration on motor imagery of walking in younger and older adults. *Neuroscience*, *222*, 49-57.
- Sirigu, A., Cohen, L., Duhamel, J. R., Pillon, B., Dubois, B., Agid, Y., & Pierrot-Deseilligny, C. (1995). Congruent unilateral impairments for real and imagined hand movements. *Neuroreport*, *6*, 997-1001.
- Slifkin, A. B. (2008). High loads induce differences between actual and imagined movement duration. *Experimental Brain Research*, *185*, 297-307.

- Tacchino, A., Bove, M., Pedulia, L., Battaglia, M., Papaxanthis, C., & Bricchetto, G. (2013). Imagined actions in multiple sclerosis patients: evidence of decline in motor cognitive prediction. *Experimental Brain Research*, *229*, 561-570.
- Tumas, V., & Sakamoto, A. C. (2009). A kinaesthetic motor imagery study in patients with writer's cramp. *Arquivos of Neuropsiquiatria*, *67*, 396-401.
- Vogt, S., Di Rienzo, F., Collet, C., Collins, A., & Guillot, A. (2013). Multiple roles of motor imagery during action observation. *Frontiers in Human Neuroscience*, doi: 10.3389/fnhum.2013.00807.
- Watson, M. E., & Rubin, D. C. (1996). Spatial imagery preserves temporal order. *Memory*, *4*, 515-534.
- Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3 Suppl.*, 1212-1217.
- Woodworth, R. S. (1899). The accuracy of voluntary movements. *Psychological Review Monograph* *3* (Suppl. 3), 1-19.
- Yardley, L., & Higgins, M. (1998). Spatial updating during rotation: the role of vestibular information and mental activity. *Journal of Vestibular Research*, *8*, 435-442.
- Young, S. J., Pratt, J., & Chau, T. (2008). Choosing the fastest movement: perceiving speed-accuracy tradeoffs. *Experimental Brain Research*, *185*, 681-688.
- Yoxon, E., Tremblay, L., & Welsh, T. N. (2015). Effect of task-specific execution on accuracy of imagined aiming movements. *Neuroscience Letters*, *585*, 72-76.
- Zelaznik, H. Z., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior*, *15*, 217-236.