Online versus Cognitive Control: A Dividing Line between Physical Action and Motor Imagery

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Abstract

Recent work has shown that motor imagery is highly sensitive to tasks that interfere with executive resources, whereas physical actions are largely immune. This has been taken as support for the Motor-Cognitive model of motor imagery, and against the theory of Functional Equivalence. Here, we examined another prediction of the MCM, namely that an opposite pattern of effects would be observed when the information available for online control was reduced. This was tested in three experiments in which participants performed either physical actions or motor imagery. The experiments manipulated the quality of information available during the online control of movement through: 1) comparing movements made with or without visual feedback; 2) comparing movements made using foveal vs. peripheral vision; and 3) comparing physical to mimed actions. All three experiments found evidence in favour of the Motor-Cognitive model in that manipulations of online control affected motor imagery but not overt action. These same results were, however, inconsistent with a Functional Equivalence view. We discuss these results in the broader context of theoretical views on perceptual vs. motor imagery.

Introduction

The human ability to generate mental images has fascinated philosophers and psychologists for centuries (Dennett, 1969; Galton, 1880; Hobbes, 1651; Pearson, 2019). Motor imagery represents a specific form of mental imagery in which an action is simulated internally without any associated body movement. In the present study, we tested the Motor-Cognitive model (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023) against the Functional Equivalence view (Jeannerod, 1995; Jeannerod & Decety, 1995).

In the Motor-Cognitive framework, both physical and imagined movements consist of a planning and execution stage (Glover, 2004). In the planning stage, motor imagery and physical actions share the same internal representations. Information originating from the environment and the body are combined with stored memories of actions to select an appropriate motor plan and form a forward model (Glover, 2004; Glover & Dixon, 2013; Kilteni et al., 2018; Shadmehr & Krakauer, 2008; Vry et al., 2012; Wolpert et al., 1998). During execution, however, motor imagery and physical action bifurcate.

In a physical action, sensory predictions from the forward model are combined with feedback; when these diverge, an error signal is sent, and unconscious online control is used to correct the movement in flight (Goodale et al., 1986; Paulignan et al., 1991; Pisella et al., 2000; Shadmehr & Krakauer, 2008; Wolpert et al., 1998). Conversely, in motor imagery the stationary condition of the body results in an absence of feedback-based online control. Rather, monitoring and elaboration of the motor image is a conscious process that depends heavily on executive functions subserved by the dorsolateral prefrontal cortex (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023). Unlike the dedicated fast visuomotor modules that underlie online control (Goodale et al., 1986; Milner & Goodale, 2006; Paulignan et al., 1991), executive resources are unequipped to simulate the fast, fine-tuned

adjustments that occur during physical movement (Nair et al., 2003), and as a consequence, motor imagery will be less accurate in reflecting the characteristics of physical action.

The Motor-Cognitive model can be contrasted with the most prominent current theory of motor imagery, known as "Functional Equivalence." This view posits that imagined movements are little more than the internal physiological and neural correlates of physical actions while overt action is inhibited (Jeannerod, 1995; Jeannerod & Decety, 1995). The notion of Functional Equivalence drew early support from findings that imagined and physical actions often share timing similarities and biomechanical constraints; for example, movements of greater duration generally also take longer to imagine (Baccarini et al., 2014; Boulton & Mitra, 2013; Decety & Jeannerod, 1995; Decety & Michel, 1989; Frak et al., 2001; Glover et al., 2005; Guillot & Collet, 2005; Jeannerod & Frak, 1999; Macuga & Frey, 2014; Papaxanthis et al., 2002; Roberts et al., 2019). Further, physiological responses such as changes in heart rate are experienced similarly during physical and imagined movement (Decety et al., 1991). Finally, large amounts of neural overlap between motor imagery and physical action have been observed in neuroimaging studies (see for review, Gerardin et al., 2000; Grèzes & Decety, 2001; Hardwick et al., 2018; Hétu et al., 2013; Jeannerod, 2008; Lotze & Halsband, 2006; Macuga & Frey, 2012).

However, numerous behavioral studies have observed large discrepancies between the characteristics of real versus imagined movements that are inconsistent with the idea of Functional Equivalence, but can be explained within the Motor Cognitive framework (Calmels & Fournier, 2001; Cerritelli et al., 2000; Decety et al., 1989; Gandrey et al., 2013; Glover et al., 2020; Glover & Baran, 2017; Grealy & Shearer, 2008; Hanyu & Itsukushima, 2000; Martel & Glover, 2023; Maruff et al., 1999; Slifkin, 2008; Wong et al., 2013; Yoxon et al., 2015, 2017). Further, at the neural level, certain brain areas show greater activation during motor imagery than during physical action, most notably the dorsolateral prefrontal cortex

(Dodakian et al., 2014; Gardini et al., 2016; Gerardin et al., 2000; Guillot et al., 2008, 2009; Lotze et al., 2003; Macuga & Frey, 2014; Stephan et al., 1995; Tacchino et al., 2017; Vry et al., 2012; Zapparoli et al., 2013), and connectivity patterns differ between physical and imagined action (Gao et al., 2011; Kim et al., 2018; Solodkin et al., 2004; Xu et al., 2014).

As stated, an important component of the Motor Cognitive model is the bifurcation of action and imagery processes during online control. Critically, motor imagery cannot use online feedback to adjust the movement in flight as occurs during physical execution. Instead, motor imagery relies heavily on executive resources to elaborate the motor image. This often results in timing discrepancies between real and imagined actions (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023; Maruff et al., 1999; Yoxon et al., 2015). For example, performing a demanding executive task, such as counting backwards by threes or generating words from a single letter, greatly slows the execution of motor imagery while only marginally affecting the timing of its physical counterpart (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023). Further, in line with the proposed role of executive functions in the Motor-Cognitive model, Martel and Glover (2023) observed that motor imagery was slowed by disruption of the dorsolateral prefrontal cortex with TMS; no such effect of TMS was observed on physical actions.

Another critical prediction of the Motor-Cognitive model, alluded to above, is that only physical actions should be sensitive to factors that impact online control, which itself depends on the quality of information available as the movement unfolds. For example, if visual feedback is removed during a movement, a physical action will slow to make greater use of proprioceptive feedback (Berthier et al., 1996; Kuhtz-Buschbeck et al., 1999; Martel & Glover, 2023; Sarlegna & Mutha, 2015; Woodworth, 1899). More generally, when the quality of information available to online control is reduced, there will be increased movement times, an increased number of in-flight adjustments, and an extended deceleration phase during

(Marteniuk et al., 1987; Meyer et al., 1988). However, within the Motor-Cognitive model, as it relies on executive resources rather than online control processes during execution, motor imagery should be impervious to these same effects. This prediction is wholly distinct from one based on the central tenet of the Functional Equivalence view whereby both physical and imagined actions operate using the same internal processes. On this analysis, motor imagery and physical actions should be similarly affected by any and all extraneous variables.

Whereas previous tests of the Motor Cognitive model focussed on the manipulations of executive functions (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023), the present study focussed on the manipulation of online control, and predicts the opposite effects. Specifically, whereas disrupting execution functions slowed motor imagery but left physical actions unaffected, here, we predicted that disrupting online control would slow physical actions but not motor imagery.

We manipulated the quality of information available to online control in three experiments. In each experiment, participants were required to either execute, or imagine executing, a reaching and placing movement under full vision vs. no vision (Experiment 1); using foveal vs. peripheral vision (Experiment 2); or when interacting with a real object vs. performing a mimed movement (Experiment 3). In the latter conditions, online control would be expected to be affected, as the information available to online processes would be reduced. For example, in Experiment 1, removing vision coincident with movement onset eliminated the use of online visual feedback of the hand and target, and thus should clearly impair normal online control processes. In Experiment 2, moving in peripheral vision reduced the acuity present in foveal vision which again should cause online control to be impaired. In Experiment 3, the lack of physical interaction with the target object in the mime condition should impair online control due to the reduction of physical interaction with the target.

If the Motor-Cognitive model is correct, in each experiment we ought to observe differences between physical actions and motor imagery. Specifically, whereas physical actions ought to be sensitive to these variables, motor imagery should not. As such, the Motor-Cognitive model predicted an interaction between the Action variable (physical vs. imagined actions) and the respective online control variables. Further, any main effects of Action whereby motor imagery took either more or less time than physical actions would be consistent only with the Motor-Cognitive model and not the Functional Equivalence view. Conversely, the only effect allowed under the Functional Equivalence model would be a main effect of online control that should be similar for both motor imagery and physical action.

Experiment 1

The first experiment explored the effects of removing visual feedback during movement on both physical action and motor imagery. As visual feedback plays a key role during online control (Glover, 2004; Meyer et al., 1988), we expected to see large effects of this manipulation on physical actions. In particular, all of movement times, time spent in deceleration, and number of online corrections should be greater when feedback is unavailable versus when it is available. If the Motor-Cognitive model is correct, these effects should be absent for motor imagery, leading to an Action (physical vs. imagery) by Vision (full vision vs. no vision) interaction. Conversely, if the Functional Equivalence view is correct, both physical and imagined movement should be equally affected by the removal of vision, and no such interaction should arise. Similarly, only the Motor-Cognitive model predicts a main effect of Action, whereby motor imagery should take longer than physical action.

Methods

Sample size and inclusion/exclusion criteria for all three experiments were determined *a priori* and were pre-registered prior to data collection alongside study rationales, procedures, data processing and analyses (https://osf.io/z7u9f). Sample size was determined as the minimum sample size that would be required to obtain a minimum 80% chance of resulting in an adjsuted likelihood ratio of at least 10:1 for both the predicted main effects and the interaction, separately for each experiment. Full datasets and scripts are available at the following link: https://osf.io/a9tzf/.

Participants

We enrolled 32 participants (25 females, tested age range 18-35 years old) from among Royal Holloway students and staff, 16 participants in each group. Two participants were replaced because they failed to follow the instructions. Participants from the undergraduate research participation pool received research credits, others received monetary reward or no compensation. All participants were right-handed by self-report, had normal or corrected-to-normal vision, had no motor or neurological impairments, and were naïve as to the exact purpose of the experiment. Due to Covid-19 safety precautions, all participants performed all tasks with a face mask and surgical gloves on. This and all other experiments presented here were approved by the College Ethics Board at Royal Holloway.

Experimental setup

The general experimental setup is shown in Figure 1 and has been used previously (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023). Participants sat comfortably at a 50 × 90 cm table set inside a large room. A computer keyboard, a wooden box (dimensions: 15.7 × 42 × 22 cm) and a small white plastic "poker chip" disc sat on top of the table. The box contained a grey plastic tube (dimensions: 15 × 4.2 cm) positioned 15 cm from the side of the box close to the participant, and the Polhemus receiver module, positioned in the corner of the box furthest from the participant. The starting position was a yellow square sticker (0.5 × 0.5 cm), positioned 52 cm away from the left side of the table, and 5 cm away from the near side. The disc was 1 cm thick and 4 cm in diameter. All other dimensions and positions were as shown in Figure 1.

For the participants who performed movements, we placed two Polhemus transmitters (7 mm in diameter) on the participant's right thumb and index fingernails to record their spatial

location in x,y,z coordinates (Polhemus Fastrak system; sampling rate: 120 Hz). Data was analysed offline.

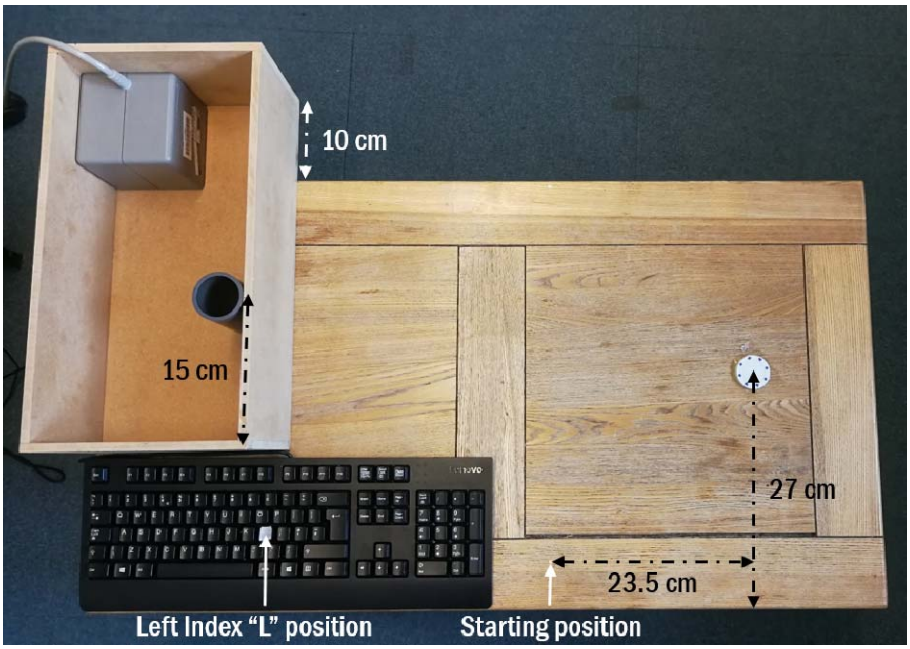

Figure 1. Experimental setup. Participants began with their right thumb and index finger on the starting position, and at a signal had to either reach to grasp the disc then place it into the grey cylinder on the left, or imagine doing so while remaining stationary. Participants used their left index finger to indicate the start and end of the movement (or its imagined counterpart) by pressing the "L" key.

Procedure

Each trial began with participants sitting with their body midline aligned with the starting mark, their right thumb and index finger in a comfortable "pinch grip" posture on this mark, and their left index finger resting on the "L" key. After a starting tone triggered via PC, participants had to reach for the disc and place it into the cylinder, or imagine doing so. In

both physical action and motor imagery groups, participants indexed the beginning and the end of their movement by pressing the “L” key with their left index finger. The physical action group performed the grasping and placing movement with their eyes either remaining open throughout (Full Vision trials) or after closing their eyes at the onset of each movement (No Vision trials). The experimenter monitored participants to ensure they followed instructions. The motor imagery group imagined reaching and placing the disc in the same two visual conditions. Participants had to imagine the action as vividly as possible, using both visual and kinaesthetic imagery of their movement experienced in the first person (i.e., to imagine seeing and feeling themselves performing the movement), while keeping their right arm/hand still on the starting position.

Each participant performed two counterbalanced blocks of 6 practice and 12 experimental trials for a total of 24 analysed trials (12 Full Vision and 12 No Vision). Trials which had to be excluded before analysis (e.g. if the participant stopped their movement during the trial, forgot to press the key, moved their hand during motor imagery, forgot to close their eyes etc.; 26/768 trials: 3.4%) were not repeated, resulting in some participants having fewer than 24 accurate trials before data processing. The experimenter continuously monitored the participants during each trial to ensure they followed instructions. In physical action trials, the experimenter put the disc back in place and participants returned to the starting position. Once the participant was set, the experimenter triggered the tone to begin the next trial.

Data processing

Keypress data. We extracted reaction time (RT) and movement time (MT) from the keypress data for both physical action and motor imagery. RT was the time between the starting tone and the first keypress (indicating the beginning of the movement/imagery). MT was the time

between first and second keypress. Any trial with RT or MT outside ± 2 IQR (Interquartile Range) for each combination of block and participant was removed from the analysis (3.4% of the total trials). As we did not make any prediction on RT, we only present the data on MT in this report (see Supplementary Information for the analysis of the RT).

Kinematic data. We extracted kinematic indices of each movement using a custom program on Python. We calculated velocity from x,y,z coordinates and filtered the data at 15 Hz with a low pass Butterworth filter of order 2. Each movement was divided into a reaching and placing phase. The beginning of the first, reaching phase was set as the point at which a minimum speed of 5cm/s was obtained, with the reaching component marked as ended at the time when the hand had again gone above a velocity of 5 cm/s after having fallen below it (or reached its minimum value), following the beginning of the first movement. This latter point also defined the beginning of the second, placing phase. The end of the placing phase was defined in the same way as the end of the reaching phase. For each of the placing and reaching phase, we also measured the time spent in deceleration (i.e., the time between the peak velocity and end of each movement phase), and the total number of online adjustments (indexed as the number of re-accelerations of the hand during the deceleration subphases and/or decelerations of the hand during acceleration subphases of each movement). Any trial with RT or MT outside ± 2 IQR (Interquartile Range) for each combination of block and participant was removed from the analysis (3.2% of the total trials).

Additionally, data obtained via the Polhemus was used to perform a manipulation check that participants were pressing the “L” key at times closely corresponding to their actual movement onset and offset. We compared RT and MT indicated by the keypresses with kinematically determined RT and three different measures of MT (see Supplementary Information).

Analyses and statistics

Data were analysed using R (R studio version: 1.4.1717, R Core Team, 2018) and nested linear mixed models (package *lme4*, Bates et al., 2015) with the evidence for competing statistical models calculated using adjusted likelihood ratios (λ_{adj}) (Glover & Dixon, 2004). Likelihood ratios represent the relative likelihood of the data given two competing models, providing a simple, intuitive index of the strength of the evidence while avoiding many of the pitfalls associated with NHST (Wasserstein & Lazar, 2016). As models with more parameters will almost always fit the data better than models with fewer parameters, adjusted likelihood ratios (λ_{adj}) were computed using the Akaike Information Criterion (Akaike, 1973). Likelihood ratios are closely related to p-values, and under typical hypothesis testing situations, a p-value of 0.05 would correspond to a $\lambda_{adj} \sim 2.7$. The use of nested linear models in combination with likelihood ratios allows for direct comparisons between models including multiple independent factors, something not directly possible using *p*-values.

To test the efficacy of our *Vision* manipulation (Full Vision/No Vision), we compared its effects on the kinematic indexes (movement time, total deceleration time, and number of online adjustments). We then used a 2x2 mixed design, with *Action* (Motor imagery/Physical action) as a between-subjects variable, and *Vision* (Full Vision/No vision) as a within-subjects variable, on the movement times as indexed by the keypresses. We implemented the maximum random effects structure for which the respective model still converged and improved model fit (Barr et al., 2013), which included a random slope for each participant when possible. We present analyses of the movement times based on keypresses. Exploratory analyses on reaction times are presented in the supplementary information.

Results

Kinematic indices

Table 1 shows the effects of Vision on the kinematic indices in the physical reaching and placing task. As expected, performing the movement without any visual guidance greatly increased movement times, time spent in deceleration phase and online adjustments of both the reaching and placing phases of physical actions (all $\lambda_{adj} > 1000$). We concluded from this that our manipulation of online control had the intended effects on physical actions. Additionally, there was very little difference between movement times when comparing the analyses of kinematics and the keypress data, suggesting that participants were overall highly accurate in indicating the beginning and end of their movements. This was shown in an additional analysis performed on kinematic MT for the physical action group vs. keypress MT for the motor imagery group which rendered the same results as in the next section (see Supplementary Information), confirming the results were not simply an artefact of the use of keypresses to index movement times in the physical action group.

Table 1. Effect of moving with full vision or no vision on kinematics.

	Full Vision (mean ± SD)	No Vision (mean ± SD)
Total movement time (ms)	1980 ± 365	4400 ± 1145
Reaching phase		
Deceleration Time (ms)	637 ± 153	1331 ± 366
Number of online adjustments	1 ± 0.7	4.5 ± 1.6
Placing phase		
Deceleration Time (ms)	743 ± 156	2437 ± 736
Number of online adjustments	1.7 ± 0.8	9.2 ± 2.9

Keypress movement times

Figure 2 shows the mean keypress movement times as a function of *Vision* and *Action* conditions. The best-fitting model of the keypress MT data included the effect of *Vision* and the *Vision* × *Action* interaction. A statistical model including an effect of *Action* only did not fit the data noticeably better than a null model (λ_{adj} = 1.8). However, adding the effect of *Vision* improved the fit greatly (λ_{adj} > 1000), and adding the interaction *Action* × *Vision* improved the fit even further (λ_{adj} > 1000), reflecting increased movement times in the no vision condition but only for the physical action group. To directly assess the Motor-Cognitive and Functional Equivalence views, we compared statistical models including the predictions made by each. A full model including both main effects and their interaction, as predicted by the Motor-Cognitive model, fit the data much better than a model including only an effect of *Vision*, as predicted by the Functional Equivalence model (λ_{adj} > 1000). In other words, the data were over 1000 times as likely when including the effects uniquely predicted by the Motor-Cognitive model than when assuming only the effect predicted by the Functional Equivalence view.

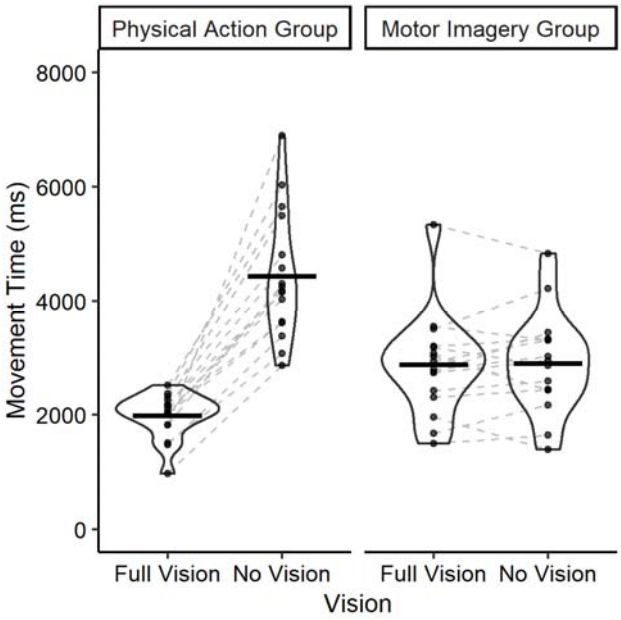

Figure 2. Effects of varying vision (Full Vision vs. No Vision) on movement times in the physical action and motor imagery groups. Individual points represent the mean score for single participants, dashed grey lines pair the means of individual participants together, and horizontal lines represent the group means. Enclosures represent the distribution of the presented data, with wider horizontal sections indicating a larger number of observations.

Discussion

In Experiment 1, the kinematic analysis confirmed that our manipulation was successful. Three separate indices of online control in physical actions, movement times, the number of online adjustments and the time spent in deceleration, were greatly increased by removing vision. The effects were most pronounced in the placing phase of the movement, which required more precision than the grasping phase. This showed that the movement times in the physical action group was related to the amount information available to online control.

The keypress data showed that whereas there were large effects of removing vision on physical actions, imagined movement times were highly similar in vision and no vision conditions. These contrasting effects of vision on imagery and physical action were consistent with the Motor Cognitive view, whereby only physical actions should be affected by manipulations that impact online control. They were not, however, compatible with a Functional Equivalence view, wherein both physical actions and motor imagery share common internal processes and so should be equally affected by extraneous variables.

Surprisingly at first glance, the predicted main effect of *Action* was not present. Although physical actions in the vision condition took less time than their imagined counterparts – itself a typical finding in this task (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023), the same movements in the no vision condition took less time in the motor imagery group than in the physical action group. In short, it would appear that the *Vision x Action* interaction obfuscated a potential main effect of *Action*. Our interpretation of these results was that the effect of removing vision on physical action was so large that movement times across both conditions averaged out to be approximately the same, and thus a main effect of *Action* was not observed.

Experiment 2

Experiment 2 provided our second test of the effects of manipulating online control on motor imagery and physical actions. Here, participants performed (or imagined performing) the movement while either being allowed to freely move their eyes and thus foveate the target (foveal condition), or while maintaining fixation on the starting point and conducting the entire movement after leaving the starting position in the visual periphery (peripheral condition). Because of the greater receptor density in the fovea versus the periphery (Jonas et

al., 1992), this manipulation ought to have predictable effects on physical action similar to, if not as powerful as, removing vision entirely. Specifically, we expected to see longer movement times, more time spent in deceleration, and a greater number of online adjustments in the peripheral than in the foveal condition. If the Motor Cognitive model is correct, the extended movement times should only arise in the physical action group and not the motor imagery group. Conversely, if the Functional Equivalence view is correct, both physical action and motor imagery should be equally affected by the manipulation.

Methods

Participants

We enrolled 60 participants (48 females, tested age range 18-44 years old) from Royal Holloway students and staff, 30 participants in each group. Two participants were replaced because of a technical error during recording. Two additional participants were replaced because they failed to follow the instructions. Inclusion criteria and Covid-19 safety precautions were the same as in Experiment 1. Sample size and inclusion/exclusion criteria were determined *a priori* as per Experiment 1, and were pre-registered prior to data collection alongside study procedures and data processing and analyses (https://osf.io/w92aj). Full dataset and scripts are available to download at the following link: https://osf.io/a9tzf/.

Experimental setup and procedure

Setup, starting position and number of trials were the same as in Experiment 1. Out of 1440 trials in total, 81 (5.6%) were excluded and not repeated due to participants m. Participants in the physical action group performed the movement while either being allowed to move their

eyes freely to foveate the target and track their hand (Foveal trials), or while being required to maintain fixation on the starting position (Peripheral trials). The experimenter continuously monitored the participants during each trial to ensure they followed instructions. The motor imagery group imagined reaching and placing the disc in the same two visual conditions. Participants had to imagine this action as vividly as possible, using both visual and kinaesthetic imagery of their movement experienced in the first person (i.e., to imagine seeing and feeling themselves performing the movement), while keeping their right arm/hand still.

Data processing

Data processing was performed exactly as in Experiment 1. In the keypress data, 3.2% of the trials had RT or MT outside ± 2 IQR (Interquartile Range) for each combination of block and were removed. In the kinematic data, the number of trials removed was 5%. Correlations between keypress and kinematic data, as well as exploratory analyses on RT can be found in the supplementary information.

Analyses and statistics

Analyses were the same as in Experiment 1, except that *Vision* condition was now broken into Foveal/Peripheral conditions rather than Vision/No Vision.

Results

Kinematic indices

Table 2 shows the effects of *Vision* on the kinematic indices in the physical reaching and placing task. As expected, performing the movement using peripheral vision increased movement times as well as time spent in deceleration and number of online adjustments in both the reaching and placing phases, compared to foveal vision (all $\lambda_{adj} > 1000$). Additionally, there was again very little difference between movement times as measured by the kinematics and the keypresses, suggesting that participants were highly accurate overall in indicating the beginning and end of the movement when pressing the keys. This was supported by an additional analysis performed on kinematic MT for the physical action group vs. keypress MT for the motor imagery group which rendered the same results as in the next section (see Supplementary Information), confirming the results were not an artefact of the use of keypresses to index movement times in the physical action group.

Table 2. Effect of using foveal or peripheral vision on kinematics.

	Foveal Vision (mean ± SD)	Peripheral Vision (mean ± SD)
Total movement time (ms)	1863 ± 344	2943 ± 782
Reaching phase		
Deceleration Time (ms)	606 ± 131	842 ± 205
Number of online adjustments	0.9 ± 0.6	2.4 ± 1.1
Placing phase		
Deceleration Time (ms)	732 ± 182	1576 ± 524
Number of online adjustments	1.3 ± 1.1	5.4 ± 2.5

Keypress movement times

Figure 3 shows the keypress movement times as a function of *Action* and *Vision* conditions. The best-fitting model of keypress MT was a full model including the effects of *Action*, *Vision* and their interaction. A stastistical model including only an effect of *Action* fit the data much better than a null model ($\lambda_{adj} = 803$), with longer movement times in the motor imagery

group than in the physical action group, consistent with what is typically observed (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023). Adding *Vision* to the model vastly improved the fit ($\lambda_{adj} > 1000$), with longer movement times in the Peripheral condition than in the Foveal condition. Finally, adding the interaction *Action* × *Vision* also greatly improved the fit ($\lambda_{adj} = 716$): the effect of *Vision* was greater in the physical action group than in the motor imagery group. As before, we also directly tested a full model including both main effects and the interaction, based on the predictions of the Motor-Cognitive theory, to a model including only an effect of *Vision*. based on the Functional Equivalence view. The statistical model representing the former was over 1000 times as likely to produce the data than the model predicted by the Functional Equivalence view ($\lambda_{adj} >1000$), again offering strong support for the Motor-Cognitive model over the Functional Equivalence view.

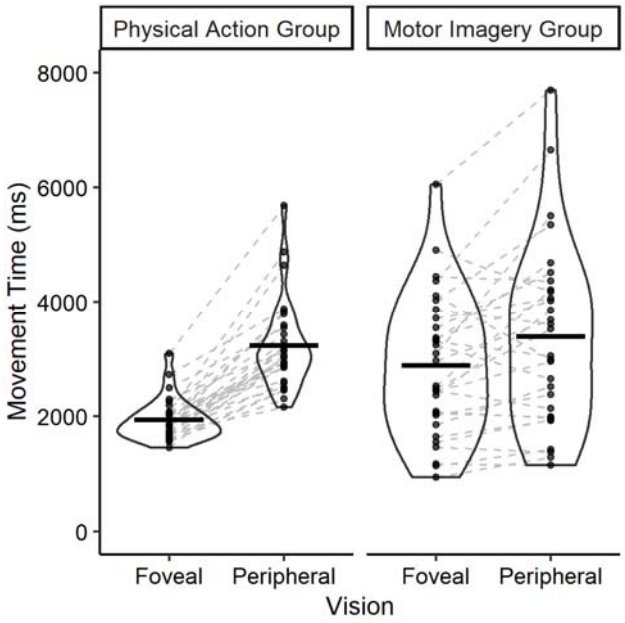

Figure 3. Effect of varying the quality of online control (Foveal vs. Peripheral) on movement times in the physical action and motor imagery groups. Conventions as in Figure 2.

Discussion

As in Experiment 1, it was clear from the kinematic data that our manipulation had the desired effect on physical actions: all of the variables including movement time, deceleration time, and number of online adjustments were greater in the peripheral vision condition than in the foveal condition. Thus, we can conclude that the overall increase in movement times in the peripheral condition were due to difficulties in using online control.

In contrast to these effects on physical actions, and consistent with the predictions of the Motor Cognitive model, we observed an interaction between *Action* and *Vision*. Moreover, unlike in Experiment 1, we also here observed a main effect of *Action* whereby movement times were greater in the motor imagery than physical action group. Both of these results strongly favour the Motor Cognitive model over the Functional Equivalence view.

Experiment 3

This experiment provided the final test of the effects of manipulating online control on motor imagery and overt action. Here, participants engaged in either the standard reaching and placing task, or a mimed version of the task using a faux disc. The *Mime* condition would be presumed to impair normal online control processes, as these are argued to rely on a physical interaction with the target in the environment (Goodale et al., 1994).

The predictions were similar to the previous experiments: If the Motor Cognitive model is correct, we would expect to see an effect of *Mime* whereby only physical actions would be affected by whether the movement was real of mimed, resulting in an *Action* by *Mime* interaction. Further, we would also expect the typical main effect of *Action*, whereby motor

imagery would take longer than physical actions. Conversely, if the Functional Equivalence view is correct, only a main effect of *Mime* should be observed.

Methods

Participants

We enrolled 60 participants (43 females, tested age range 18-43 years old) from Royal Holloway students and staff, 30 participants in each group. Four participants were replaced because they failed to follow the instructions. Inclusion criteria and Covid-19 safety precautions were the same as in Experiments 1 and 2. Sample size and inclusion/exclusion criteria were determined *a priori* and were pre-registered prior to data collection alongside study procedures and data processing and analyses (https://osf.io/ws2zn). Full dataset and scripts are available to download at the following link: https://osf.io/a9tzf/.

Experimental setup and procedure

Setup, starting position and number of trials were the same as in Experiments 1 and 2 for one of the conditions ("Control"; see left panel of Figure 4). For the second condition ("Mime"), in place of the disc was a paper circle faux disc fastened to the table using tape, in the usual location of the disc. The real disc was placed 12 cm to the right of the faux disc (centre to centre, i.e. space of 8 cm between the paper and the real discs, see right panel of Figure 4) so that participants could see it clearly during their tasks.

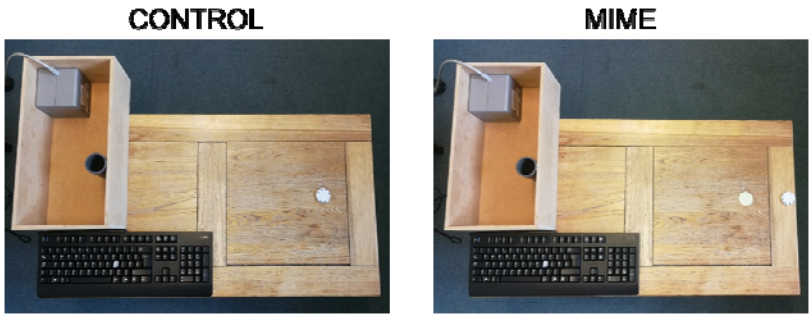

Figure 4. Experimental setup for the Control and the Mime conditions. In the mime condition, the disc was moved 12 cm to the right (centre to centre) and replaced by an identically-sized circle of white paper.

One group of participants performed the physical action under normal conditions (Control trials) or by pantomiming the action (Mime trials). This latter condition consisted in performing the same movement but using the faux disc: participants reached towards the faux disc and moved their (empty) fingers towards the cylinder. The second group imagined reaching and placing the faux disc in the same two conditions. The experimenter continuously monitored the participants during each trial to ensure they followed instructions. Out of 1440 trials in total, 53 (3.7%) were excluded and not repeated due to participants' mistakes such as movement during motor imagery, participants forgetting to press the button.

Data processing

Data processing was performed exactly as in Experiment 1 and 2. In the keypress data, 3.2% of the trials had RT or MT outside ± 2 IQR (Interquartile Range) for each combination of block and were removed. In the kinematic data, the number of trials removed was 2.8%.

Analyses and statistics

Analyses were the same as in Experiments 1 and 2, except that the *Mime* condition replaced the *Vision* condition as the within-subjects variable.

Results

Kinematic indices

Table 3 shows the effects of *Mime* on the kinematic indices in the physical reaching and placing task. There was strong evidence that performing the mimed action increased overall movement times (λ_{adj} = 63). The evidence for an increase in time spent in the deceleration phase during the placing phase was more moderate (λ_{adj} = 5.9), whereas evidence for an increase in the number of online adjustments during the placing phase was strong (λ_{adj} = 14.2). However, neither time spent in deceleration during the reaching phase (λ_{adj} = 1.3), nor the number of online adjustments during the reaching phase were noticeably different between conditions (λ_{adj} = 1.9); these particular results were at odds with our predictions of an effect of *Mime* on online control. Overall, these results suggest that our manipulation had much more modest effects on online control than were present in Experiments 1 and 2. As before, there was very little difference between movement times indicated by the kinematics and the keypress, suggesting that participants were accurate in indicating the beginning and end of the movement. This is in accordance with an additional analysis performed on kinematic MT for the physical action group vs. keypress MT for the motor imagery group which rendered the same results as in the next section (see Supplementary Information).

Table 3. Effect of performing a movement on kinematics in the Control and Mime conditions.

	Control (mean ± SD)	Mime (mean ± SD)
Total movement time (ms)	2072 ± 492	2355 ± 742
Reaching phase		
Deceleration Time (ms)	679 ± 185	749 ± 327
Number of online adjustments	1.3 ± 1.0	1.8 ± 1.9
Placing phase		
Deceleration Time (ms)	795 ± 192	879 ± 287
Number of online adjustments	1.7 ± 1.1	2.2 ± 1.1

Keypress movement times

Figure 5 shows the effects of *Action* and *Mime* on keypress movement times. The best-fitting model of keypress MT included the main effects of *Action* and *Mime*, but no interaction. A stastistical model including an effect of *Action* fit the data much better than a null model (λ_{adj} = 449), with longer movement times in the motor imagery group than in the physical action group. Adding a main effect of *Mime* moderately improved the fit (λ_{adj} = 7.5), with longer movement times in the mime condition than in the control condition. Contrary to the prediction of the Motor-Cognitive model, adding the interaction *Action* × *Mime* did not improve the fit (λ_{adj} = 0.97). Nonetheless, the data overall were again more consistent with the Motor-Cognitive model than with the Functional Equivalence view: A full model including the effects of *Action, Mime,* and their interaction fit the data much better than a model including only a main effect of *Mime,* (λ_{adj} = 433). That is, the data were 433 times as likely to arise when assuming all of the effects predicted by the Motor-Cognitive model than when assuming the only effect allowed by the Functional Equivalence view.

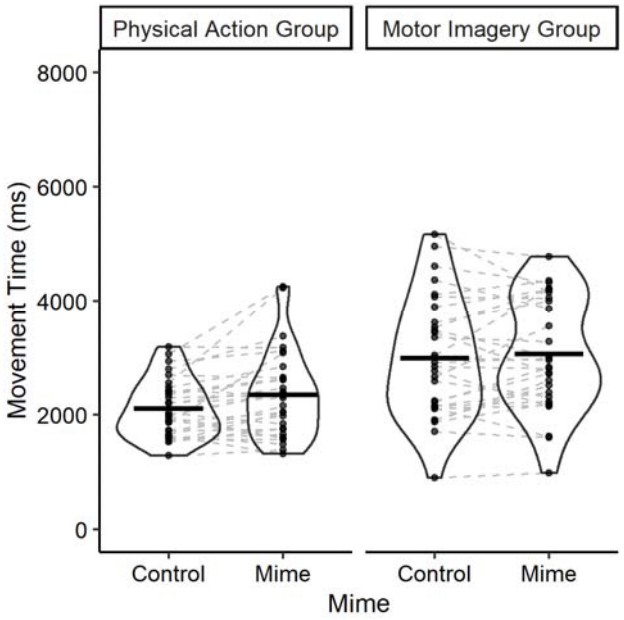

Figure 5. Effect of varying the quality of online control (Control vs. Mime) on movement times in the physical action and motor imagery groups. Conventions as in Figure 2.

Discussion

The kinematic data in Experiment 3 was less compelling than in the previous two experiments. Although there was moderate-to-good evidence that three of the five kinematic indices were affected by the Mime condition, for the other two indices the evidence was inconclusive. As such, it seems fair to conclude that the *Mime* manipulation had a smaller effect on online control than either the no vision or the peripheral vision manipulations in the first two experiments.

Although imagined movement times were longer than physical movement times, the predicted *Action* × *Mime* interaction did not arise. Overall, however, the pattern of results was more

consistent with the Motor Cognitive model than the Functional Equivalence view, due to the large main effect of *Action*.

A possible explanation for the lack of evidence for an *Action* × *Mime* interaction was that the effect of *Mime* was small compared to the comparable manipulations of online control used in the other two experiments. As a consequence, although the pattern of means was consistent with *Mime* having a greater effect on physical actions than on motor imagery, with an effect of 240 msec on physical action compared to 70 msec for motor imagery, the statistical evidence for the interaction was lacking. It is possible the predicted interaction is present but much smaller than we had predicted, and may require a larger sample size to be reliably detected.

General Discussion

Keypress movement time data in all three experiments supported the Motor Cognitive model over the Functional Equivalence model. Critically, participants who imagined the movements were consistently unaffected by the manipulations that impacted online control, in line with the predictions of the Motor-Cognitive model. However, physical actions were affected by these same variables (although the evidence for this in Experiment 3 was modest). Overall, these results are incompatible with the view of physical action and motor imagery being Functionally Equivalent.

Whereas the key interactions between *Action* and online control were highly evident in Experiments 1 and 2, in Experiment 3 the smaller and less consistent effects of our manipulation on online control made it hard to discern if an interaction between *Action* and *Mime* was present, resulting in a lack of clear evidence either favouring or refuting an interaction. We conclude from this that the impact on online control in this experiment was insufficient to allow clear evidence of the interaction, although the effect of *Action*, uniquely predicted by the Motor-Cognitive model, was still present. It may be the case that online control is not as severely disrupted by miming a movement as has been previously argued (Goodale et al., 1994).

The present study represents part of a larger experimental dissociation between motor imagery and physical action. In previous work, we demonstrated that numerous variables, including precision, cognitive load, and disruption of the dorsolateral prefrontal cortex with TMS, all affected the timing of motor imagery to a much greater degree than physical actions (Glover et al., 2020; Glover & Baran, 2017; Martel & Glover, 2023). Here, we have shown the opposite pattern: variables that affect physical action may not always affect motor imagery. Although either pattern of effects alone might be argued to arise as an artefact of the

reaching and placing paradigm we are using, it seems *prima facie* extremely unlikely for such an artefact to produce opposing patterns of results depending on the manipulations employed. Further, our control analyses showed that the keypress movement times for physical actions closely corresponded to the kinematic measures of same, again refuting the idea of an artefact producing the results. We thus conclude that not only are there clear differences between motor imagery and physical action, but the processes are in fact largely if not wholly independent during execution.

Limitations

At least two critiques of the present study may be offered. First, although the effects of vision in Experiment 2 were consistent with the predictions of the Motor-Cognitive model, they were nonetheless somewhat at odds with a recent study which found that eye movements did affect motor imagery in an aiming task, and that it affected physical movement in the opposite way (Pathak et al., 2023). Many discrepancies exist between the present study and this study, however, that may explain this apparent discrepancy. Crucially, the Fitt's type task used by Pathak et al. does not emphasize online control but rather focuses on planning the movement through feedforward strategies, whereas the present study focuses on a change in the quality of online control, making the two studies not comparable.

Second, all three experiments in the present study had a between-subjects design in which participants performed either motor imagery or physical actions. As practice strengthens the motor representation available for motor imagery (Yoxon et al., 2015), participants in the motor imagery group might have lacked sufficient experience to form a vivid motor image. Indeed, large order effects were observed in our previous study when using a within-subjects design wherein participants performed both motor imagery and the corresponding physical

action (Martel & Glover, 2023; Experiment 1). Our view was that within the present paradigm, order effects could potentially mask important results (similar to how the main effect of *Action* was masked by the interaction with *Vision* in Experiment 1), and so we chose to use the simpler between-subjects design. Nonetheless, it is an interesting and important question whether and to what degree physical experience on a task may reduce the observed discrepancies between motor imagery and physical action.

Theories of Imagery: Perceptual Imagery vs. Motor Imagery

A consideration of the commonalities between motor imagery and other types of imagery, such as visual imagery, may be informative in considering how imagery operates. Arguably, all forms of imagery require the internal generation of a phenomenological experience with reduced or absent perceptual inputs. Presumably the generation of these images would be largely based on memory traces which are then elaborated on internally to develop a more detailed image.

Interestingly, similar to the Functional Equivalence view, early models of perceptual imagery offered the notion that imagery and perception were largely similar both neurologically and experientially (Kosslyn et al., 2001). Within these frameworks, the experience of imagery (whether perceptual or motoric) is largely a passive process that arises out of the activation of similar brain structures to its physical counterpart. In short, these earlier views held that imagery was largely driven by bottom-up processes, relatively independent of higher cognition.

However, researchers in perceptual imagery have since come to believe that top-down influences play a critical role in the generation of imagery (Dijkstra et al., 2017; Mechelli et al., 2004). If true, this would imply that motor imagery might also be largely an active, top-

down process. In line with this, the Motor-Cognitive model contends that the generation and elaboration of a mental image depend heavily on executive resources in the DLPFC, and that this becomes more pronounced as memory becomes less vivid, or in the case or motor imagery specifically, when online control processes make memory less relevant to the task. Consistent with this interpretation, both motor and perceptual imagery are often associated with increased activity in the DLPFC, relative to their real-world counterparts (Gardini et al., 2016; Gerardin et al., 2000; Guillot et al., 2008, 2009; Herholz et al., 2012; Lotze et al., 2003; Macuga & Frey, 2014; Mellet et al., 1995; Vry et al., 2012; Yoo et al., 2003; Zapparoli et al., 2013). Further, disruption of the DLPFC using TMS has been shown to specifically impair motor imagery but not physical action (Martel & Glover, 2023).

Following calls for further theoretical development in motor imagery research (Dietrich, 2008; Guillot et al., 2012; Moran et al., 2012; O'Shea & Moran, 2017), the field has recently seen the introduction of several promising theoretical frameworks (e.g., Bach et al., 2022; Frank et al., 2023; Hurst & Boe, 2022), many of which reference a perception-action link akin to that which forms the basis of ideomotor theory (Hommel et al., 2001). Along with these other developments, we believe that with continued testing and refinement, the Motor-Cognitive model may contribute towards a more modern, sophisticated account of motor imagery.

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Competing Interests

There are no conflicts of interest.

Data availability statement

All data, code and material used in this study are available on the website of the Open Science Framework (OSF) at the following link: https://osf.io/a9tzf/.

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