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

Marie Martel[1], Scott Glover[1]

[1] Department of Psychology, Royal Holloway University of London

Running title: Online control in motor imagery

Corresponding author:

Dr Marie Martel

Dept. of Psychology

Royal Holloway University of London

Egham, Surrey, TW20 0EX

marie.martel@rhul.ac.uk

Abstract

Motor imagery has long been characterised as the internal experience of the silent unfolding of motor processes, known as the Functional Equivalence view. We argue that a stronger account of motor imagery incorporates how it differs from physical action, as encapsulated in the Motor-Cognitive model. The Motor-Cognitive model argues that in lieu of online control, motor imagery is elaborated using cognitive processes relying on executive resources. We tested the Motor-Cognitive and Functional Equivalence models in experiments that manipulated the quality of information available during movement through 1) removing vision; 2) restricting vision to the periphery; or 3) miming the movement. All three experiments found strong evidence in favour of the Motor-Cognitive model and against the Functional Equivalence view. We discuss these results in the broader context of the processes involved in mental imagery.

Introduction

The human propensity to generate internal mental images has fascinated philosophers and psychologists for centuries[1–4]. Motor imagery represents a specific form of mental imagery in which an action is simulated internally without any associated body movement. The most prominent current theory of motor imagery, known as "Functional Equivalence", posits that imagined movements are little more than the internal physiological and neural correlate of physical actions wherein the actions themselves have been inhibited[5,6]. This theory drew early support from findings that imagined and physical actions often share timing similarities and biomechanical constraints; for example, longer duration movements generally also take longer to imagine[7–17]. Further, physiological responses such as changes in heart rate are experienced similarly during physical and imagined movement[18]. Finally, large amounts of neural overlap between motor imagery and physical action have been observed in neuroimaging studies (see for review[19–25]).

In opposition to the notion of functional equivalence, however, numerous studies have observed large discrepancies between the timing and affordances of real versus imagined movements[26–39]. Further, at the neural level, certain brain areas show greater activation during motor imagery than during physical action, most notably the dorsolateral prefrontal cortex[15,19,40–48], and connectivity patterns differ between physical and imagined action[49–52], raising serious doubts as to the degree to which motor imagery and physical action can be described as functionally equivalent.

Given the vital importance of motor imagery to training and rehabilitation[53–59], and the numerous divergences of findings from the Functional Equivalence view, it is important to develop more sophisticated and precise models of how motor imagery relates to physical action. In the present study, we test a new model of motor imagery, the Motor-Cognitive Model[30,31,34]. In this account, both physical and imagined movements consist of a planning and execution stage[60]. In the planning stage, motor imagery and physical actions share the same internal representations. Information originating from the environment and the body are paired with stored memories of actions to select an appropriate motor plan and form a forward model[47,60–64]. During execution, however, motor imagery and physical

action bifurcate. In a physical action, sensory predictions are combined with feedback; when these diverge, an error signal is sent, and unconscious online control is used to correct the movement in flight[63–67]. Conversely, in motor imagery there is no feedback-based online control as the body remains stationary. Rather, monitoring and elaboration of the motor image is a conscious process that depends heavily on executive functions subserved by the dorsolateral prefrontal cortex[30,31,34]. Unlike the dedicated fast visuomotor modules that subserve online control[65,66,68], executive resources are unequipped to simulate the fine-tuned adjustments that occur during physical movement[69].

Consequently, when generating a motor image of a movement whose physical execution would rely heavily on online control processes, motor imagery must in its turn rely heavily on executive resources, and discrepancies will emerge between real and imagined actions[30,31,34,35,38]. Evidence for this comes from studies showing that 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[30,31,34]. Further, in line with the proposed role of executive functions in the Motor-Cognitive Model, Martel and Glover[34] observed that participants took longer to imagine a movement after disruption of their dorsolateral prefrontal cortex with TMS.

A key tenet of the Motor-Cognitive model that follows from the bifurcation of physical and imagined action during execution is that only physical actions should be sensitive to variables that impact online control. Under most circumstances, the brain uses fast visual and proprioceptive feedback loops to monitor and adjust actions in flight[60,63,70]. However, in some situations, these systems may suffer from a paucity of information. For example, if visual feedback is removed during a movement, the physical action will slow to make greater use of proprioceptive feedback[34,71–74]. More generally, when the quality of information available to online control is reduced, there is a corresponding reduction in the efficiency of online control, resulting in the movement requiring an increased number of in-flight adjustments and increased movements times with an extended deceleration phase during physical actions[70,75]. However, within the Motor-Cognitive model, motor imagery should be impervious to these same effects. This prediction is wholly distinct from one based on the concept of functional

equivalence, whereby both physical and imagined actions operate using the same internal processes, and as such should be equally affected by all variables.

In the present study, we manipulated the availability of information to online control in three reaching and placing experiments. In each experiment, participants were required to either execute, or imagine executing, a movement under full vision vs. no vision (Experiment 1); foveal vs. peripheral vision (Experiment 2); or when interacting with a real object vs. performing a mimed movement (Experiment 3). In the latter of all of the above-named 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 impaired normal online control processes that occur under full vision. In Experiment 2, moving in peripheral vision reduced the acuity present in foveal vision which again caused online control to be impaired. In Experiment 3, the lack of physical interaction with the target object in the mime condition impaired online control as it reduced the somatosensory information.

If the Motor-Cognitive model is correct, in each experiment we ought to observe differences between physical actions and motor imagery in their respective responses to manipulations affecting online control. Specifically, whereas physical actions ought to be sensitive to these variables, motor imagery should not. As such, one would expect an interaction between the Action variable (physical vs. imagined actions) and the respective online control variables if the Motor-Cognitive model is correct. Conversely, if the Functional Equivalence model is correct, then both physical actions and motor imagery should be similarly affected by all manipulations affecting online control, resulting in no such interactions. Further, any main effects of Action would be consistent only with the Motor-Cognitive model and not the Functional Equivalence view, as the latter would assume similar timings across the two behaviours. The only effect allowed under the Functional Equivalence model is a main effect of online control that should be similar for both motor imagery and physical action.

Results

Experiment 1

Keypress movement times

The best-fitting model of the data included the effect of *Vision* and the *Vision* × *Action* interaction. A statistical model including only an effect of *Action* did not fit the data noticeably better than a null model (λ_{adj} = 1.8), however, adding the effect of *Vision* (λ_{adj} > 1000) improved the fit greatly, and adding the interaction *Action* × *Vision* (λ_{adj} > 1000) further improved the fit, reflecting increased movement times in the no vision condition but only for the physical action group (Figure 1). 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 assuming the effects uniquely predicted by the Motor-Cognitive model than when assuming only the effect predicted by the Functional Equivalence view.

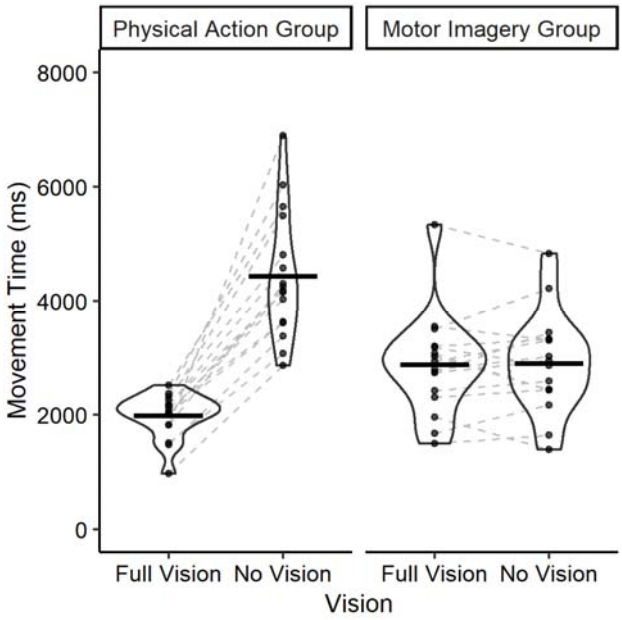

Figure 1. Effects of varying vision (Full Vision vs. No Vision) on movement times in the physical action and motor imagery groups. Individual points represent the mean score for single participants, dashed grey lines pairing means of individual participants together, and horizontal lines represent the group means. Enclosures represent the distribution of the presented data, with wider horizontal sections indicating a larger number of observations.

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 reaching and placing phase of physical actions (all $\lambda_{adj} > 1000$). We concluded from this that our manipulation of online control had the intended effects on physical actions.

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

Experiment 2

Keypress movement times

The best-fitting model was a full model including the effects of *Action*, *Vision* and their interaction (Figure 2). A stastistical model including only an effect of *Action* fit the data much better than a null model (λ_{adj} = 803), with longer movement times in the motor imagery group than in the physical action group, consistent with what is usually observed[30,31,34]. Adding *Vision* to the model further improved the fit (λ_{adj} > 1000), with longer movement times in the Peripheral condition than in the Foveal condition, a finding in the opposite direction to what we predicted. Finally, adding the interaction *Action* × *Vision* vastly improved the fit (λ_{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 (λ_{adj} >1000), again offering strong support for the Motor-Cognitive model over the Functional Equivalence view.

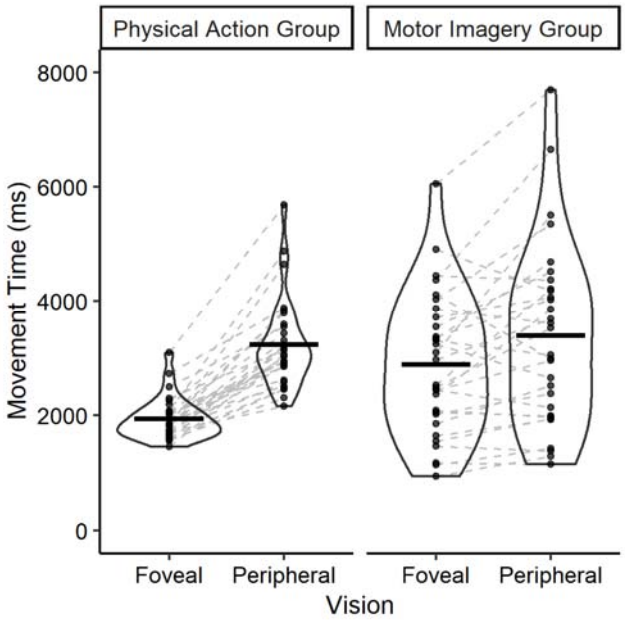

Figure 2. Effect of varying the quality of online control (Foveal vs. Peripheral) on movement times in the physical action and motor imagery groups. Conventions as in Figure 1.

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, time spent in deceleration phase and online adjustments of both reaching and placing phase compared to foveal vision (all $\lambda_{adj} > 1000$). This showed that our manipulation of vision had its intended effects on physical actions.

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

Experiment 3

Keypress movement times

The best-fitting model included only the main effects of *Action* and *Mime* (Figure 3). 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 our prediction, 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 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 the effects uniquely predicted by the Motor-Cognitive model than when assuming only the effect predicted by the Functional Equivalence view.

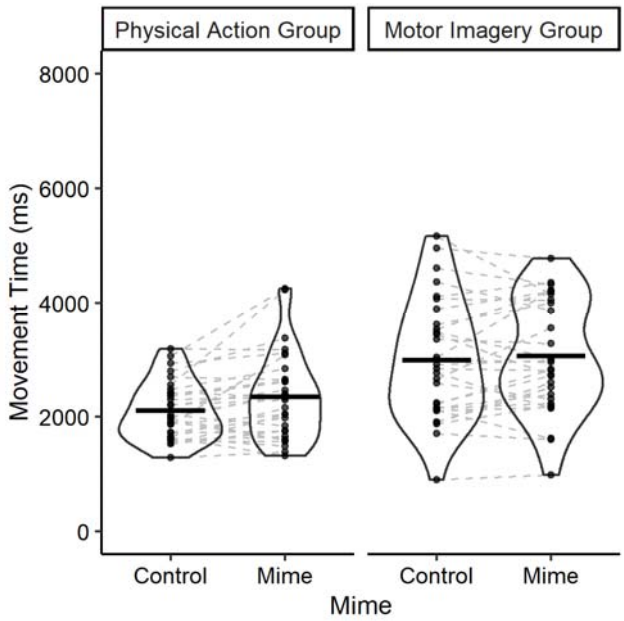

Figure 3. Effect of varying the quality of online control (Control vs. Mime) on movement times in the physical action and motor imagery groups. Conventions as in Figure 1.

Kinematic indices

Table 3 shows the effects of *Mime* on the kinematic indices in the physical reaching and placing task. Performing the mimed action increased overall movement times (λ_{adj} = 63), time spent in deceleration phase during the placing phase (λ_{adj} = 5.9), and the number of online adjustments during the placing phase (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 results were at odds with our predictions for kinematics. Overall however, our results still suggest that our manipulation worked (albeit not as strongly as those in Experiments 1 and 2), and that there was evidence for a difference in the indices of online control between the control condition and the mime condition.

Table 3. Effect of performing a movement with a real object or miming it on kinematics.

	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

Discussion

Keypress movement time data in all three experiments supported the Motor Cognitive model over the Functional Equivalence model. Critically, the data in all three experiments were much more consistent with the predictions of the Motor-Cognitive model than they were with the predictions of the Functional Equivalence view. Participants who imagined the movements were consistently unaffected by the manipulations that impacted online control, consistent with the predictions of the Motor-Cognitive model. These results militate against any simplistic view of physical action and motor imagery as being functionally equivalent.

Some aspects of the results were unexpected. First, in Experiment 1 the predicted main effect of *Action* was eliminated by the interaction between *Action* and *Vision*: Physical actions in the vision condition took less time than their imagined counterparts – itself a typical finding in this task[30,31,34], yet the same actions in the no vision condition took less time in the motor imagery group than in the physical action group. Despite being unanticipated, this result yet supports the notion inherent in the Motor-Cognitive model that physical action but not motor imagery would be affected by the manipulation of online control. Second, we had predicted an effect of *Action* in the opposite direction to that observed in Experiment 2, anticipating that the movement times in the peripheral condition would be so slowed in the physical action group that it would lead to a similar overpowering of the main effect as observed in Experiment 1. However, the crucial aspect of the finding was the existence of any difference between physical action and motor imagery, as this can only arise under the Motor-Cognitive model. Finally, whereas the key interactions between *Action* and the manipulations of 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 disputing 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.

A key difference between physical actions and motor imagery, as revealed in the present study, is that only the former employs online visual and proprioceptive feedback during execution. Interestingly, the online processes that arise during physical action have been shown to be both automatic and unconscious[65–67]. In contrast, as motor imagery is a mental process that seeks to reproduce the phenomenology of physical action, it is perhaps unsurprising that imagery is unable to recreate the subtle fine-tuning of actions that arise from unconscious online processes: Not only is there no feedback from which to simulate these online adjustments in movement, there is no conscious access to the internal processes that generate them. Indeed, whereas participants in the physical action conditions often noticeably struggled to perform the movements when either visual feedback or foveal

vision of the hand/target was removed, none of the participants in the motor imagery task expressed any increase in difficulty in imagining movements under these conditions, and nor were their imagined movements noticeably affected. This supports the tenet of the Motor-Cognitive model that a clear divergence of physical action and motor imagery occurs during execution.

A broader comparison that may be useful in the present context is between motor imagery and perceptual (e.g., visual) imagery. In the latter, current theory suggests that top-down influences play a critical role in the absence of bottom-up inputs[76,77]. This suggests that a central process in any imagery task, be it perceptual or motor imagery, is to generate conscious mental simulations based on memory and to elaborate on them in order to create as vivid and realistic a mental image as possible. We contend that both 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 in either perceptual or motor imagery, 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[15,19,41–44,47,48,78–80].

Similar to the Functional Equivalence view, early models of perceptual imagery proffered the simplistic notion that imagery and perception were largely similar both neurologically and phenomenologically [81]. Theories of perceptual imagery have since evolved to become much more sophisticated, with modern views including a prominent role for top-down cognitive processes[4,76,77]. However, this evolution of theory has largely been absent in the domain of motor imagery, despite calls for further theoretical development[82–85]. The present study thus represents a step in the process of moving towards a modern theory of motor imagery.

Methods

Experiment 1

Sample size and inclusion/exclusion criteria were determined *a priori* and were pre-registered prior to data collection alongside study procedures, data processing and analyses (https://osf.io/z7u9f). Full dataset 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. 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 4 and has been used previously[30,31,34]. 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 4.

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.

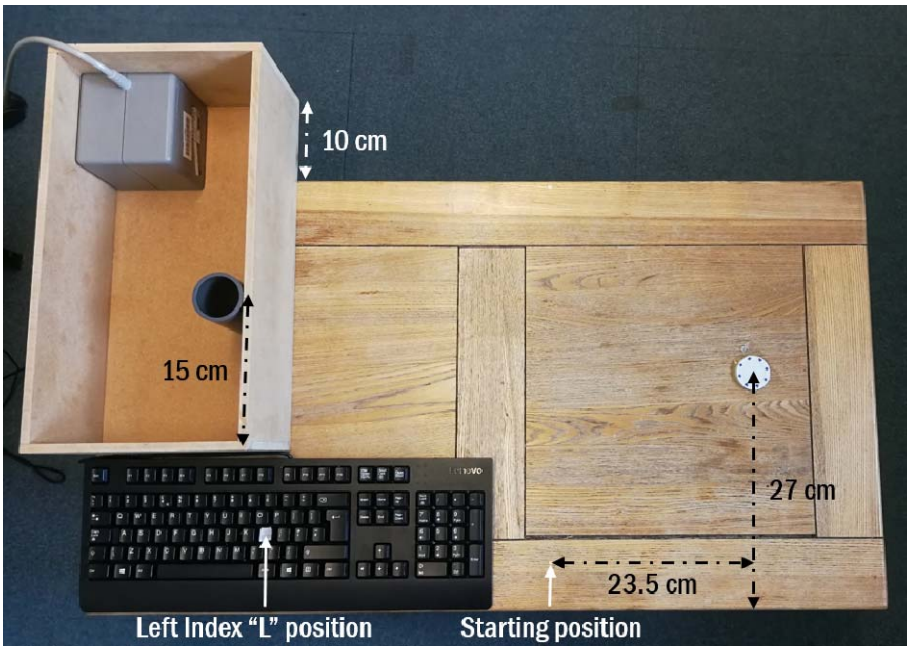

Figure 4. Experimental setup. Participants began with their right thumb and index finger on the starting position, and at a signal had to either reach to grasp the disc then place it into the grey cylinder on the left, or imagine doing so while remaining stationary. Participants used their left index 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 still.

Each participant performed two counterbalanced blocks of 6 practice trials and 12 experimental for a total of 24 analysed trials (Full Vision or No Vision). Trials which had to be excluded before analysis (e.g. if the participant stopped their movement during the trial, participant forgot to press the key, etc.) were not repeated. 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 the reach to place movement using a custom program on Python. The beginning of the 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

placing phase. The end of the placing movement was defined in the same way as the end of the reaching movement. For each of the placing and reaching movements, 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 phases and/or decelerations of the hand during acceleration phases 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 thus compared RT and MT indicated by the keypresses with kinematically determined RT and three different MT (see Supplementary Information).

Analyses and statistics

Data was analysed with R (R studio version: 1.4.1717[86]) using nested linear mixed models (package *lme4*[87]*)* with the evidence for competing statistical models calculated using adjusted likelihood ratios (λ_{adj})[88]. 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[89]. 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[90]. 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 different factors, something not directly possible using conventional *p*-values.

We 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. We implemented the maximum random effects structure for which the respective model still converged and improved model fit [91], which includes 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.

Additionally, 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).

Experiment 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/w92aj). Full dataset and scripts are available to download at the following link: https://osf.io/a9tzf/.

Participants

We enrolled 60 participants (48 females, tested age range 18-44 years old) from Royal Holloway students and staff. 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.

Experimental setup and procedure

Setup, starting position and number of trials were the same as in Experiment 1. 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 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.

Experiment 3

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/.

Participants

We enrolled 60 participants (43 females, tested age range 18-43 years old) from Royal Holloway students and staff. 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.

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 5). For the second condition ("Mime"), in place of the shown disc was a paper disc taped on the table. The real disc was placed 12 cm to the right of the paper disc (centre to centre, i.e. space of 8 cm between the paper and the real discs, see right panel of Figure 5) so that participants could see it clearly during their tasks.

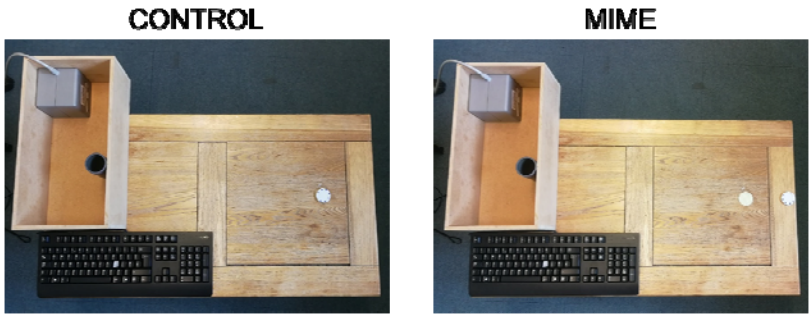

Figure 5. Experimental setup for the Control and the Mime conditions. In the mime condition, the disc was moved 12 cm to the right (centre to centre) and replaced by an identically-sized circle of white paper.

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 an imaginary disc: participants reached towards paper "disc" and moved their (empty) fingers towards the cylinder. The second group imagined reaching and placing the disc in the same two conditions. The experimenter continuously monitored the participants during each trial to ensure they followed instructions.

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.

Acknowledgments

This work was supported by the Leverhulme Trust (grant number RPG-2020-225).

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/.

References

1. Dennett, D. The Nature of Images and the Introspective Trap. Reprinted in Ned Block (1981) Imagery. (1969).
2. Galton, F. Statistics of mental imagery. *Mind* **5**, 301–318 (1880).
3. Hobbes, T. *Leviathan*. (London, 1651).
4. Pearson, J. The human imagination: the cognitive neuroscience of visual mental imagery. *Nat Rev Neurosci* **20**, 624–634 (2019).
5. Jeannerod, M. Mental imagery in the motor context. *Neuropsychologia* **33**, 1419–1432 (1995).
6. Jeannerod, M. & Decety, J. Mental motor imagery: a window into the representational stages of action. *Curr. Opin. Neurobiol.* **5**, 727–732 (1995).
7. Baccarini, M. *et al.* Tool use imagery triggers tool incorporation in the body schema. *Front. Psychol.* **5**, 492 (2014).
8. Boulton, H. & Mitra, S. Body posture modulates imagined arm movements and responds to them. *J. Neurophysiol.* **110**, 2617–2626 (2013).
9. Decety, J. & Jeannerod, M. Mentally simulated movements in virtual reality: does Fitts's law hold in motor imagery? *Behav. Brain Res.* **72**, 127–134 (1995).

10. Decety, J. & Michel, F. Comparative analysis of actual and mental movement times in two graphic tasks. *Brain Cogn.* **11**, 87–97 (1989).
11. Frak, V., Paulignan, Y. & Jeannerod, M. Orientation of the opposition axis in mentally simulated grasping. *Exp. Brain Res.* **136**, 120–127 (2001).
12. Glover, S., Dixon, P., Castiello, U. & Rushworth, M. F. S. Effects of an orientation illusion on motor performance and motor imagery. *Exp. Brain Res.* **166**, 17–22 (2005).
13. Guillot, A. & Collet, C. Duration of mentally simulated movement: a review. *J. Mot. Behav.* **37**, 10–20 (2005).
14. Jeannerod, M. & Frak, V. Mental imaging of motor activity in humans. *Curr. Opin. Neurobiol.* **9**, 735–739 (1999).
15. Macuga, K. L. & Frey, S. H. Differential contributions of the superior and inferior parietal cortex to feedback versus feedforward control of tools. *Neuroimage* **92**, 36–45 (2014).
16. Papaxanthis, C., Pozzo, T., Skoura, X. & Schieppati, M. Does order and timing in performance of imagined and actual movements affect the motor imagery process? The duration of walking and writing task. *Behav. Brain Res.* **134**, 209–215 (2002).
17. Roberts, J. W., Welsh, T. N. & Wakefield, C. J. Examining the equivalence between imagery and execution - Do imagined and executed movements code relative environmental features? *Behav. Brain Res.* **370**, 111951 (2019).
18. Decety, J., Jeannerod, M., Germain, M. & Pastene, J. Vegetative response during imagined movement is proportional to mental effort. *Behav. Brain Res.* **42**, 1–5 (1991).
19. Gerardin, E. *et al.* Partially overlapping neural networks for real and imagined hand movements. *Cereb. Cortex* **10**, 1093–1104 (2000).
20. Grèzes, J. & Decety, J. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum Brain Mapp* **12**, 1–19 (2001).
21. Hardwick, R. M., Caspers, S., Eickhoff, S. B. & Swinnen, S. P. Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. *Neurosc.i Biobehav. Rev.* **94**, 31–44 (2018).

22. Hétu, S. *et al.* The neural network of motor imagery: an ALE meta-analysis. *Neurosci. Biobehav. Rev.* **37**, 930–949 (2013).

23. Jeannerod, M. *Motor Cognition: what actions tell the self. Motor Cognition* (Oxford University Press, 2008).

24. Lotze, M. & Halsband, U. Motor imagery. *J. Physiol. Paris* **99**, 386–395 (2006).

25. Macuga, K. L. & Frey, S. H. Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. *Neuroimage* **59**, 2798–2807 (2012).

26. Calmels, C. & Fournier, J. F. Duration of physical and mental execution of gymnastic routines. *Sport Psychol.* **15**, 142–150 (2001).

27. Cerritelli, B., Maruff, P., Wilson, P. & Currie, J. The effect of an external load on the force and timing components of mentally represented actions. *Behav. Brain Res.* **108**, 91–96 (2000).

28. Decety, J., Jeannerod, M. & Prablanc, C. The timing of mentally represented actions. *Behav. Brain Res.* **34**, 35–42 (1989).

29. Gandrey, P., Paizis, C., Karathanasis, V., Gueugneau, N. & Papaxanthis, C. Dominant vs. nondominant arm advantage in mentally simulated actions in right handers. *J. Neurophysiol.* **110**, 2887–2894 (2013).

30. Glover, S., Bibby, E. & Tuomi, E. Executive functions in motor imagery: support for the motor-cognitive model over the functional equivalence model. *Exp. Brain Res.* **238**, 931–944 (2020).

31. Glover, S. & Baran, M. The motor-cognitive model of motor imagery: evidence from timing errors in simulated reaching and grasping. *J. Exp. Psychol. Hum. Percept. Perform.* **43**, 1359–1375 (2017).

32. Grealy, M. A. & Shearer, G. F. Timing processes in motor imagery. *Eur. J. Cogn. Psychol.* **20**, 867–892 (2008).

33. Hanyu, K. & Itsukushima, Y. Cognitive distance of stairways: a multi-stairway investigation. *Scand. J. Psychol.* **41**, 63–70 (2000).

34. Martel, M. & Glover, S. TMS over dorsolateral prefrontal cortex affects the timing of motor imagery but not overt action: Further support for the motor-cognitive model. *Behavioural Brain Research* **437**, 114125 (2023).

35. Maruff, P. *et al.* Asymmetries between dominant and non-dominant hands in real and imagined motor task performance. *Neuropsychologia* **37**, 379–384 (1999).

36. Slifkin, A. B. High loads induce differences between actual and imagined movement duration. *Exp. Brain Res.* **185**, 297–307 (2008).

37. Wong, L., Manson, G. A., Tremblay, L. & Welsh, T. N. On the relationship between the execution, perception, and imagination of action. *Behav. Brain Res.* **257**, 242–252 (2013).

38. Yoxon, E., Tremblay, L. & Welsh, T. N. Effect of task-specific execution on accuracy of imagined aiming movements. *Neurosci. Lett.* **585**, 72–76 (2015).

39. Yoxon, E., Pacione, S. M., Song, J.-H. & Welsh, T. N. The action-specific effect of execution on imagination of reciprocal aiming movements. *Hum. Mov. Sci.* **54**, 51–62 (2017).

40. Dodakian, L., Stewart, J. C. & Cramer, S. C. Motor imagery during movement activates the brain more than movement alone after stroke: a pilot study. *J. Rehabil. Med.* **46**, 843–848 (2014).

41. Gardini, S. *et al.* Brain activation patterns characterizing different phases of motor action: execution, choice and ideation. *Brain Topogr* **29**, 679–692 (2016).

42. Guillot, A. *et al.* Functional neuroanatomical networks associated with expertise in motor imagery. *Neuroimage* **41**, 1471–1483 (2008).

43. Guillot, A. *et al.* Brain activity during visual versus kinesthetic imagery: an fMRI study. *Hum. Brain Mapp.* **30**, 2157–2172 (2009).

44. Lotze, M., Scheler, G., Tan, H.-R. M., Braun, C. & Birbaumer, N. The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *Neuroimage* **20**, 1817–1829 (2003).

45. Stephan, K. M. *et al.* Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *J. Neurophysiol.* **73**, 373–386 (1995).

46. Tacchino, A. *et al.* Motor imagery as a function of disease severity in multiple sclerosis: an fMRI study. *Front. Hum. Neurosci.* **11**, 628 (2017).

47. Vry, M.-S. *et al.* Ventral and dorsal fiber systems for imagined and executed movement. *Exp. Brain Res.* **219**, 203–216 (2012).

48. Zapparoli, L. *et al.* Mental images across the adult lifespan: a behavioural and fMRI investigation of motor execution and motor imagery. *Exp. Brain Res.* **224**, 519–540 (2013).

49. Gao, Q., Duan, X. & Chen, H. Evaluation of effective connectivity of motor areas during motor imagery and execution using conditional Granger causality. *Neuroimage* **54**, 1280–1288 (2011).

50. Kim, Y. K., Park, E., Lee, A., Im, C.-H. & Kim, Y.-H. Changes in network connectivity during motor imagery and execution. *PLoS One* **13**, e0190715 (2018).

51. Solodkin, A., Hlustik, P., Chen, E. E. & Small, S. L. Fine Modulation in Network Activation during Motor Execution and Motor Imagery. *Cereb. Cortex* **14**, 1246–1255 (2004).

52. Xu, L. *et al.* Motor execution and motor imagery: A comparison of functional connectivity patterns based on graph theory. *Neuroscience* **261**, 184–194 (2014).

53. Bello, U. M., Winser, S. J. & Chan, C. C. H. Role of kinaesthetic motor imagery in mirror-induced visual illusion as intervention in post-stroke rehabilitation. *Rev. Neurosci.* **31**, 659–674 (2020).

54. Guillot, A. & Collet, C. Construction of the Motor Imagery Integrative Model in Sport: a review and theoretical investigation of motor imagery use. *Int. Rev. Sport Exerc. Psychol.* **1**, 31–44 (2008).

55. Jackson, P. L., Lafleur, M. F., Malouin, F., Richards, C. & Doyon, J. Potential role of mental practice using motor imagery in neurologic rehabilitation. *Arch. Phys. Med. Rehabil.* **82**, 1133–1141 (2001).

56. Malouin, F. & Richards, C. L. Mental practice for relearning locomotor skills. *Phys. Ther.* **90**, 240–251 (2010).

57. Mulder, T. Motor imagery and action observation: cognitive tools for rehabilitation. *J. Neural Transm. (Vienna)* **114**, 1265–1278 (2007).

58. Ruffino, C., Papaxanthis, C. & Lebon, F. Neural plasticity during motor learning with motor imagery practice: Review and perspectives. *Neuroscience* **341**, 61–78 (2017).

59. Sharma, N., Pomeroy, V. M. & Baron, J.-C. Motor imagery: a backdoor to the motor system after stroke? *Stroke* **37**, 1941–1952 (2006).

60. Glover, S. Separate visual representations in the planning and control of action. *Behav. Brain Sci.* **27**, 3–24 (2004).

61. Glover, S. & Dixon, P. Context and vision effects on real and imagined actions: support for the common representation hypothesis of motor imagery. *J. Exp. Psychol. Hum. Percept. Perform.* **39**, 1352–1364 (2013).

62. Kilteni, K., Andersson, B. J., Houborg, C. & Ehrsson, H. H. Motor imagery involves predicting the sensory consequences of the imagined movement. *Nat. Commun.* **9**, 1617 (2018).

63. Shadmehr, R. & Krakauer, J. W. A computational neuroanatomy for motor control. *Exp. Brain Res.* **185**, 359–381 (2008).

64. Wolpert, D. M., Miall, R. C. & Kawato, M. Internal models in the cerebellum. *Trends Cogn. Sci. (Regul. Ed.)* **2**, 338–347 (1998).

65. Goodale, M. A., Pelisson, D. & Prablanc, C. Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature* **320**, 748 (1986).

66. Paulignan, Y., MacKenzie, C., Marteniuk, R. & Jeannerod, M. Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Exp Brain Res* **83**, 502–512 (1991).

67. Pisella, L. *et al.* An 'automatic pilot' for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia. *Nat. Neurosci.* **3**, 729–736 (2000).

68. Milner, D. & Goodale, M. *The Visual Brain in Action*. (OUP Oxford, 2006).

69. Nair, D. G., Purcott, K. L., Fuchs, A., Steinberg, F. & Kelso, J. A. S. Cortical and cerebellar activity of the human brain during imagined and executed unimanual and bimanual action sequences: a functional MRI study. *Brain Res Cogn Brain Res* **15**, 250–260 (2003).

70. Meyer, D. E., Abrams, R. A., Kornblum, S., Wright, C. E. & Smith, J. E. Optimality in human motor performance: ideal control of rapid aimed movements. *Psychol Rev* **95**, 340–370 (1988).

71. Berthier, N. E., Clifton, R. K., Gullapalli, V., McCall, D. D. & Robin, D. J. Visual Information and Object Size in the Control of Reaching. *J Mot Behav* **28**, 187–197 (1996).

72. Kuhtz-Buschbeck, J. P., Boczek-Funcke, A., Illert, M., Joehnk, K. & Stolze, H. Prehension movements and motor development in children. *Experimental Brain Research* **128**, 65–68 (1999).

73. Sarlegna, F. R. & Mutha, P. K. The influence of visual target information on the online control of movements. *Vision Research* **110**, 144–154 (2015).

74. Woodworth, R. S. Accuracy of voluntary movement. *The Psychological Review: Monograph Supplements* **3**, i–114 (1899).

75. Marteniuk, R. G., MacKenzie, C. L., Jeannerod, M., Athenes, S. & Dugas, C. Constraints on human arm movement trajectories. *Can J Psychol* **41**, 365–378 (1987).

76. Dijkstra, N., Zeidman, P., Ondobaka, S., van Gerven, M. a. J. & Friston, K. Distinct Top-down and Bottom-up Brain Connectivity During Visual Perception and Imagery. *Sci Rep* **7**, 5677 (2017).

77. Mechelli, A., Price, C. J., Friston, K. J. & Ishai, A. Where Bottom-up Meets Top-down: Neuronal Interactions during Perception and Imagery. *Cerebral Cortex* **14**, 1256–1265 (2004).

78. Herholz, S. C., Halpern, A. R. & Zatorre, R. J. Neuronal Correlates of Perception, Imagery, and Memory for Familiar Tunes. *Journal of Cognitive Neuroscience* **24**, 1382–1397 (2012).

79. Mellet, E., Tzourio, N., Denis, M. & Mazoyer, B. A Positron Emission Tomography Study of Visual and Mental Spatial Exploration. *Journal of Cognitive Neuroscience* **7**, 433–445 (1995).

80. Yoo, S.-S., Freeman, D. K., McCarthy, J. J. I. & Jolesz, F. A. Neural substrates of tactile imagery: a functional MRI study. *NeuroReport* **14**, 581–585 (2003).

81. Kosslyn, S. M., Ganis, G. & Thompson, W. L. Neural foundations of imagery. *Nat Rev Neurosci* **2**, 635–642 (2001).

82. Dietrich, A. Imaging the imagination: the trouble with motor imagery. *Methods* **45**, 319–324 (2008).

83. Guillot, A., Hoyek, N., Louis, M. & Collet, C. Understanding the timing of motor imagery: recent findings and future directions. *Int. Rev. Sport Exerc. Psychol.* **5**, 3–22 (2012).

84. Moran, A., Guillot, A., MacIntyre, T. & Collet, C. Re-imagining motor imagery: building bridges between cognitive neuroscience and sport psychology. *Br. J. Psychol.* **103**, 224–247 (2012).

85. O'Shea, H. & Moran, A. Does motor simulation theory explain the cognitive mechanisms underlying motor Imagery? A critical review. *Front. Hum. Neurosci.* **11**, 72 (2017).

86. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. (2018).

87. Bates, D., Mächler, M., Bolker, B. & Walker, S. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* (2015) doi:10.18637/jss.v067.i01.

88. Glover, S. & Dixon, P. Likelihood ratios: a simple and flexible statistic for empirical psychologists. *Psychon. Bull. Rev*. **11**, 791–806 (2004).

89. Wasserstein, R. L. & Lazar, N. A. The ASA statement on p-values: context, process, and purpose. *Am. Stat.* **70**, 129–133 (2016).

90. Akaike, H. Information theory and an extension of the maximum likelihood principle. in *B. N. Petrove & F. Csaki (Eds.), Second international symposium on information theory* 267–281 (1973).

91. Barr, D. J., Levy, R., Scheepers, C. & Tily, H. J. Random effects structure for confirmatory hypothesis testing: Keep it maximal. *J Mem Lang* **68**, (2013).