



Incongruent imagery interferes with action initiation

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ABSTRACT

It has been suggested that representing an action through observation and imagery share neural processes with action execution. In support of this view, motor-priming research has shown that observing an action can influence action initiation. However, there is little motor-priming research showing that imagining an action can modulate action initiation. The current study examined whether action imagery could prime subsequent execution of a reach and grasp action. Across two motion analysis tracking experiments, 40 participants grasped an object following congruent or incongruent action imagery. In Experiment 1, movement initiation was faster following congruent compared to incongruent imagery, demonstrating that imagery can prime the initiation of grasping. In Experiment 2, incongruent imagery resulted in slower movement initiation compared to a no-imagery control. These data show that imagining a different action to that which is performed can interfere with action production. We propose that the most likely neural correlates of this interference effect are brain regions that code imagined and executed actions. Further, we outline a plausible mechanistic account of how priming in these brain regions through imagery could play a role in action cognition.

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1. Introduction

It has been proposed that observing or imagining an action engages similar neural processes as those used in execution of that same action (James, 1890; Jeannerod, 1994; Prinz, 1997). Lending support to this idea, neuroimaging studies have identified a comparable network of brain regions that are active during execution, observation and imagination of actions (Grèzes & Decety, 2001). This network includes the inferior frontal gyrus (IFG) and inferior parietal lobule (IPL), which constitute the human mirror neuron system (MNS) (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010), and other regions associated with the control of action such as the supplementary motor area (SMA) and cingulate motor area (CMA) (Grèzes & Decety, 2001; Jeannerod, 2001; Munzert, Lorey, & Zentgraf, 2009).

There are numerous hypotheses that suggest why such a co-active mechanism might exist, which include action understanding (Fogassi et al., 2005; Iacoboni et al., 2005; Rizzolatti, Fogassi, & Gallese, 2001), action prediction (Prinz, 1997; Wilson & Knoblich, 2005), and mindreading (Gallese & Goldman, 1998). One account argues that the shared processing between action perception and production provides a means of “tuning” the motor system

through repeated internal simulation (Jeannerod, 1994; Prinz, 1997). According to this hypothesis, activation of corresponding brain structures through mental simulation should prime action execution.

Testing these predictions, Kilner, Paulignan, and Blakemore (2003) theorised that if the motor system is activated by observed movements, interference should occur when observing a different action to one that is simultaneously executed. Kilner et al. (2003) recorded sinusoidal arm movements of participants whilst they observed somebody else simultaneously perform congruent, incongruent or no arm movements (control). Consistent with their hypothesis, variance in arm movement was significantly greater when observing incongruent movement compared to control; no other condition differed from control. Thus, observation interfered with action production, which is consistent with other datasets (Brass, Bekkering, & Prinz, 2001; Dijkerman & Smit, 2007; Kilner, Hamilton, & Blakemore, 2007). Observation has also been shown to facilitate action production (Brass, Bekkering, Wohlschlagel, & Prinz, 2000), though most studies that showed an action-priming effect did not include a relevant baseline, which means facilitation and interference are equally plausible explanations of the data (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Edwards, Humphreys, & Castiello, 2003; Heyes, Bird, Johnson, & Haggard, 2005). Together, these motor-priming data have been argued to be evidence for a ‘motor

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contagion' when performing and observing actions (Blakemore & Frith, 2005). That is, the motor system of the observer is primed to produce the observed movement.

Based on similar shared motor processes between imagery and execution, there is evidence to support a similar line of theorising for imagery as observation. Imagined actions share neural substrates with execution (Grèzes & Decety, 2001; Jeannerod, 2001; Munzert et al., 2009) and are organised somatotopically in premotor and parietal cortices (Ehrsson, Geyer, & Naito, 2003). Consequently, imagined actions modulate muscle activity in the specific muscles that are used in the execution of the same movements (Fadiga et al., 1999). In addition to neural properties, imagery also shares functional properties with execution (Decety, 1996; Guillot & Collet, 2005). For example, breathing and cardiac frequency have been shown to increase when athletes imagine performing in a competitive environment (Gallego, Denot-Ledunois, Vardon, & Perruchet, 1996), and imagined movements follow the same biomechanical constraints as actual movements (Johnson, 2000). These lines of evidence suggest that imagery and execution share neural and functional processes (Decety, 1996; Grèzes & Decety, 2001; Jeannerod, 2001).

Further evidence for shared processes between imagery and action production has been provided by studies that show imagery and action production have a direct influence on each other. Imagery training facilitates a wide range of motor tasks (Allami, Paulignan, Brovelli, & Boussaoud, 2008; Boschker, Bakker, & Rietberg, 2000; Louis, Guillot, Maton, Doyon, & Collet, 2008; Yáñez et al., 1998), including complex sports performance (for reviews, see Cumming & Ramsey, 2008; Feltz & Landers, 1983; Murphy, Nordin, & Cumming, 2008) and muscle strength (Ranganathan, Siemionow, Liu, Sahgal, & Yue, 2004; Yue & Cole, 1992). These findings show that repeated imagery training can result in longer-term benefits to motor performance. In addition, action production has been shown to have a direct influence on imagery performance (Schwartz & Holton, 2000; Sirigu & Duhamel, 2001; Wexler, Kosslyn, & Berthoz, 1998; Wohlschläger & Wohlschläger, 1998). For example, in a mental rotation task, performing a congruent hand rotation produced faster response times and less errors than performing an incongruent hand rotation (Wexler et al., 1998). Together, these findings show that imagery can assist in skill acquisition and that performing an incongruent action interferes with imagery.

Taken together, these findings support the suggestion that observation and imagery share neural and functional processes with action production. Consequently, observing or imagining an action can influence action production (Jeannerod, 1994; Prinz, 1997). To date, numerous studies have shown a motor-priming effect from observing congruent compared to incongruent actions (Brass et al., 2000, 2001; Castiello et al., 2002; Craighero et al., 2002; Dijkerman & Smit, 2007; Edwards et al., 2003; Heyes et al., 2005; Kilner et al., 2003, 2007). However, similar motor-priming evidence, which shows that the congruency of an imagined action influences the performance of an action, has not yet been provided. As a result, although it is clear that repeated sessions of imagery (imagery training) can influence action production (Allami et al., 2008; Boschker et al., 2000; Louis et al., 2008; Murphy et al., 2008; Ranganathan et al., 2004; Yáñez et al., 1998) it is not known whether imagery, like observation, automatically primes the motor system for action. Based on the evidence for shared motor processes between imagery, observation and execution, similar motor-priming predictions follow for imagery as observation (e.g., Kilner et al., 2003). That is, imagining a different action to that which is performed should interfere with performance. By contrast, imagining a similar action should not cause interference and may facilitate performance.

To test these predictions, two experiments were performed using a similar design to that used by Jackson, Jackson, and Rosicky

(1995) to study non-target interference effects. Jackson et al. (1995) presented a target object alone or alongside a non-target object, and the task for each trial was to reach and grasp the target. For both experiments in the current paper the general setup was similar: a target object was presented alongside one or two non-target objects (Fig. 1). Experiment 1 was performed to establish that action imagery could prime the initiation of grasping. One of two target objects was presented between two non-target objects. On each trial participants grasped the target object and the time taken to initiate movement was recorded. Prior to performing the grasp, participants imagined grasping the target object (congruent) or one of the non-target objects (incongruent). If imagery does prime the initiation of grasping, we would expect shorter reaction times following congruent compared to incongruent imagery.

In Experiment 2, a no-imagery control condition was added to the experimental procedures in order to examine the direction of performance modulation. If congruent imagery reduced the time taken to initiate grasping compared to control, this would suggest congruent imagery facilitated grasping. By contrast, if incongruent imagery increased the time taken to initiate grasping compared to control, this would suggest incongruent imagery interfered with grasping. If both predictions are substantiated then this pattern of results would be consistent with a prior behavioural observation study, which also showed facilitation and interference to performance (Brass et al., 2000). By contrast, if imagery only interferes with action, these data will be consistent with data that only showed an interference effect from observation (Brass et al., 2001; Dijkerman & Smit, 2007; Kilner et al., 2003, 2007).

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty participants (18 male), aged between 18 and 32 years (mean = 22.8 years, $SD = 3.4$), took part in the experiment. All were right handed (as determined by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected to normal vision. Ethical approval was gained through the local ethics board.

2.1.2. Apparatus

A dual camera MacReflex infrared 3D motion analysis tracking system (50 Hz) was used to record the initiation of movement

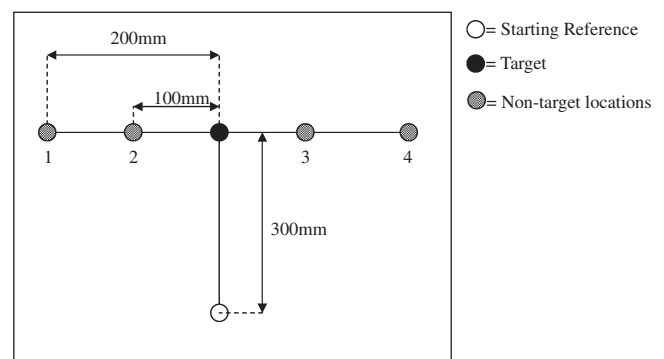


Fig. 1. The experimental setup. Experiment 1: On near configuration trials two non-targets were presented in locations 2 and 3. On far configuration trials two non-targets were presented in locations 1 and 4. On every trial one of two target objects (small or large) was presented in the same central location. Experiment 2: On each trial one non-target was presented in one of the four non-target locations (1–4). The target object was presented in the same central location on every trial. The general procedure was the same for both experiments. Participants first performed an experimental condition (Experiment 1: congruent or incongruent imagery; Experiment 2: congruent, incongruent or no imagery), before reaching and grasping the target object.

performance. A reflective marker (1 cm diameter) was attached to each participant's wrist (medial side). Reaction time data were analysed using Microsoft Excel. Two target objects were used (height, 50 mm), which had different diameters (small, 25 mm; large, 50 mm) and two non-targets were used, which were the same size (height, 100 mm; diameter, 25 mm). All objects were wooden cylinders.

Plato Spectacles (Translucent Technologies) were used to regulate each participant's vision. The lenses are filled with liquid crystal creating an opaque lens that can be cleared by an electric charge in order to allow vision (with the change to clear taking 1 ms). A PC computer that was able to simultaneously operate the spectacles and trigger the motion analysis recording was used.

The testing table surface was covered with white paper and a circular disc (10 mm in diameter) was placed 30 mm from the table edge and used as the starting position of movement. The target object was placed 300 mm directly in front of the start position on all trials and the non-target objects were placed in two of the four locations on each trial: 100 mm (near configuration) or 200 mm (far configuration) directly to the left and right of the target object (Fig. 1).

2.1.3. Procedure

Participants were given the Edinburgh Handedness Inventory (Oldfield, 1971) to screen for right-hand dominance and then wore the Plato Spectacles for the remainder of the experiment. Before each trial the Plato Spectacles were opaque. At the start of each trial, the spectacles became clear for 1 s and the participant viewed the stimuli configuration for that trial (i.e., position of the two non-target objects and target object size). Following this period, the spectacles returned to opaque for 5 s, during which time participants were instructed by the experimenter to either imagine grasping the target object (congruent imagery) or imagine grasping one of the non-target objects (incongruent imagery). Before the experiment, participants were instructed to perform imagery from a first-person perspective. That is, imagine that they were performing the task from within their own body with their right hand (Morris, Spittle, & Watt, 2005). In the incongruent imagery condition, they could choose which of the two non-targets they imagined grasping. When the spectacles became clear for a second time, participants were required to grasp the target object. Participants were instructed to grasp the object at a 'natural' speed (i.e., not as fast as possible). The motion capture equipment recorded the initiation of movement for every grasp.

2.1.4. Design

There were three independent variables, resulting in a 2 (imagery condition: congruent vs. incongruent) \times 2 (non-target configuration:

near vs. far) \times 2 (target size: small vs. large) design. Four repetitions per trial type were conducted, for a total of 32 trials, the order of which were randomised within one block of trials. The number of trials performed in the current study was reduced to ensure that participants were able to perform the imagery as instructed. We expected that more trials would lead to boredom or mental fatigue and dilute the influence of imagery. To counter a potential problem with statistical power, we tested twice the number of participants than is typical in these paradigms and replicated the results across two experiments.

2.1.5. Data analysis

Reaction time (ms) was defined as the point when the velocity of the wrist marker exceeded 25 mm per second. Any trials that were three standard deviations away from the overall mean were discarded from data analysis (<5% in both experiments, respectively). The motion capture system did not recognise the reflective marker during one participant's trials, so these trials were removed from the analysis. The data were analysed using a 2 (imagery condition) \times 2 (non-target configuration) \times 2 (target size) repeated measures ANOVA.

2.2. Results

There was a significant effect of imagery condition $F(1, 18) = 15.73, p < 0.01$. Participants were faster to initiate their movements following congruent than incongruent imagery. There were no effects of non-target configuration $F(1, 18) = 0.56, p = 0.465$, target size $F(1, 18) = 2.29, p = 0.148$, and no significant interactions (Fig. 2).

2.3. Discussion

Movement initiation was shorter following congruent imagery compared to incongruent imagery, which demonstrates imagery can prime execution. This finding is consistent with previous motor-priming data that showed observation could prime execution (Brass et al., 2000, 2001; Castiello et al., 2002; Craighero et al., 2002; Dijkerman & Smit, 2007; Edwards et al., 2003; Heyes et al., 2005; Kilner et al., 2003, 2007). However, the design of Experiment 1 did not permit the direction of modulation to be determined. It is unclear whether congruent imagery facilitated movement initiation, incongruent imagery interfered with movement initiation or both occurred. In Experiment 2, a no-imagery baseline condition was added to delineate the direction of modulation. In addition, the experimental setup was simplified in two ways. First, because no effects were found concerning target size, the same target object was used in all trials. Second, in order to be certain which non-target participants performed their incongruent imagery

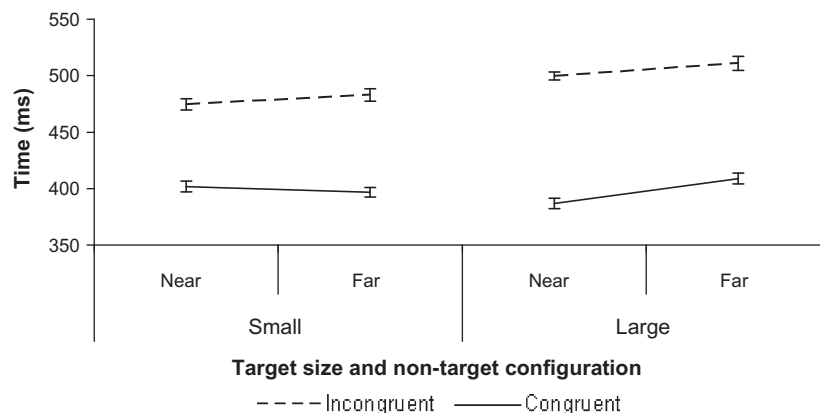


Fig. 2. Mean reaction time data for Experiment 1 (ms \pm SEM). Movement initiation was faster following congruent imagery compared to incongruent imagery. There were no effects of target size or non-target configuration and no interactions.

towards, only one non-target was presented in all trials (instead of two).

3. Experiment 2

3.1. Introduction

The aim of the second experiment was to determine the direction of performance modulation. To do so, a no-imagery baseline was added. If congruent imagery facilitated movement initiation, it was hypothesised that movement initiation would be reduced following congruent imagery compared to no imagery. Alternatively, if incongruent imagery interfered with movement performance, it was hypothesised that movement initiation would be longer following incongruent imagery compared to no imagery.

3.2. Methods

3.2.1. Participants

Twenty participants (14 male), aged between 20 and 32 years ($M = 22$ years, $SD = 3.2$) took part in the experiment, all of whom had not completed Experiment 1. All were right handed (as determined by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected to normal vision.

3.2.2. Apparatus

The large target object from Experiment 1 was removed in Experiment 2; instead, the small target object was used exclusively. In addition, one non-target object (instead of two) was presented on each trial in one of the four non-target locations (Fig. 1). No other changes were made to the materials used from Experiment 1.

3.2.3. Procedure

The experiment was conducted over two separate testing sessions. Session 1 consisted of the baseline measure (no-imagery), which was performed in one block. The procedure was identical to Experiment 1 except participants were not instructed to perform imagery. Instead, they were told to grasp the target when the goggles became clear. On a subsequent day (no more than 1 week later), participants completed Session 2, which was identical to Experiment 1.

3.2.4. Design

There were three independent variables, resulting in a 3 (imagery condition: congruent vs. incongruent vs. no imagery) \times 2 (non-

target configuration: near vs. far) \times 2 (non-target side: left vs. right) design. Four trials per trial type were conducted, making a total of 48 trials per participant. In Session 1, the order of non-target configuration and non-target side were randomised in one block (16 trials). In Session 2, the order of imagery condition (congruent vs. incongruent), non-target configuration and non-target side were randomised in one block of 32 trials.

3.2.5. Data analysis

Reaction time (ms) was measured in the same fashion as Experiment 1 and analysed using a 3 (imagery condition) \times 2 (non-target configuration) \times 2 (non-target side) repeated measures ANOVA.

3.2.6. Results and discussion

There was a significant effect of imagery condition $F(2, 38) = 7.79$, $p < 0.01$. A Bonferroni comparison of means showed that participants were slower to initiate movements following incongruent imagery compared to congruent and no imagery (Fig. 3). There were no effects of non-target configuration $F(1, 19) = 1.57$, $p = 0.225$, non-target side $F(1, 19) = 0.01$, $p = 0.976$ and no significant interactions. These results demonstrate that incongruent imagery interferes with the initiation of grasping.

4. General discussion

The current work demonstrates that imagining a different action to that which is performed interferes with action execution. Our findings show that similar to observation (Brass et al., 2001; Dijkerman & Smit, 2007; Kilner et al., 2003, 2007), incongruent imagery can interfere with action production. Blakemore and Frith (2005) interpreted action-interference from observation as a form of motor contagion: the motor system of the observer is primed to produce the observed movement. A similar interpretation can be applied to the current data: imagining an action primes the motor system to produce that action. This would explain the interference to action production from imagining a different action to the performed action. Taken together, these data support the hypothesis that representing an action through imagery or observation can “tune” the motor system by engaging the same neural processes as action execution (Jeannerod, 1994; Prinz, 1997).

4.1. Shared motor processes for imagery and execution

The current findings support the idea that imagery and execution share common motor processes (James, 1890; Jeannerod,

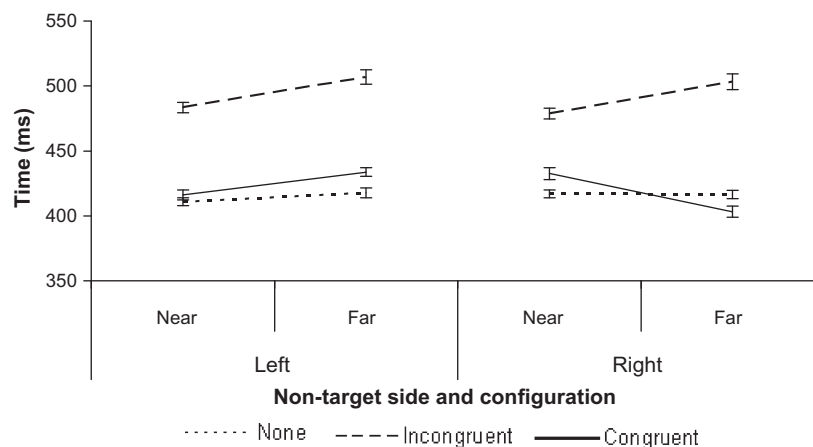


Fig. 3. Mean reaction time data for Experiment 2 (ms \pm SEM). Movement initiation was slower following incongruent imagery compared to congruent and no imagery. There were no effects of non-target side or non-target configuration and no interactions.

1994; Prinz, 1997) by demonstrating that the congruency of an imagined action can influence the production of action. Specifically, action initiation was delayed following imagined actions that were incongruent to subsequent action production. This finding extends previous studies that demonstrate imagery training can facilitate performance of visuo-motor and sporting tasks (Allami et al., 2008; Cumming & Ramsey, 2008; Feltz & Landers, 1983; Murphy et al., 2008; Yáñez et al., 1998), to show that imagining an action automatically primes the motor system to produce even simple, well-learned tasks, such as reaching and grasping. This is consistent with the motor-contagion effect from action observation (Blakemore & Frith, 2005). That is, observing an action automatically primes the motor system to produce that action (Brass et al., 2000, 2001; Castiello et al., 2002; Craighero et al., 2002; Dijkerman & Smit, 2007; Edwards et al., 2003; Heyes et al., 2005; Kilner et al., 2003, 2007). Taken together, these data suggest that observing or imagining an action automatically primes the motor system to produce that action, even when your own action is predetermined.

4.2. An interference effect

The pattern of results in the current study using imagery is consistent with the majority of observation data that shows an interference effect to action production (Brass et al., 2001; Dijkerman & Smit, 2007; Kilner et al., 2003, 2007). Indeed, in the motor-priming literature, few behavioural studies have shown both facilitation and interference with action observation (but see Brass et al., 2000). Thus, converging evidence from observation and imagery shows stronger support for interference than facilitation in motor-priming experiments. One interpretation of these data is that congruent action representations, whether engaged via observation or imagery, activate similar motor processes as execution and require no inhibition. Consequently, there is no cost to performance as measured by an interference effect. By contrast, incongruent action representations may activate dissimilar motor processes that need to be inhibited, or that interfere with a performed action, thus resulting in action-interference (Brass et al., 2001). However, under certain conditions, such as more complex visuo-motor tasks, sports performance, music and dance, imagery more consistently facilitates motor performance (Allami et al., 2008; Cumming & Ramsey, 2008; Feltz & Landers, 1983; Murphy et al., 2008; Yáñez et al., 1998). Therefore, facilitation to motor performance is possible with more difficult tasks or when the amount of imagery is increased. It may be that for well-learned tasks, such as reaching and grasping, ceiling effects limit the opportunity to measure facilitative effects. Future work that clarifies the conditions under which facilitation and interference occur would further inform the function of shared processing between imagery and execution.

The action-interference effect previously demonstrated with observation (Brass et al., 2000, 2001; Dijkerman & Smit, 2007; Kilner et al., 2003, 2007) has been argued to result from interference within a common neural network for observed and executed actions (Blakemore & Frith, 2005). Brain imaging research has shown that a comparable network of brain regions responds during imagined and executed movements (Grèzes & Decety, 2001). Furthermore, like observed actions (Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), imagined actions have a somatotopic organisation (Ehrsson et al., 2003) and modulate muscle activity in the specific muscles that are used in the execution of the same movements (Fadiga et al., 1999). Thus, it is possible that the neural substrate for action-interference with imagery is located in a common neural network for imagined and executed actions, which include IFG, IPL, SMA and CMA (Grèzes & Decety, 2001; Jeannerod, 2001; Munzert et al., 2009).

Another explanation of the interference effect is that incongruent imagery modulated visual attention onto task-irrelevant cues (i.e., a non-target object). In support of this, eye movements have been shown to reflect the content of the imagined scene (Brandt & Stark, 1997). However, explanations that discount motor-priming completely do not seem convincing. Evidence for neural and functional similarity between imagery and execution is robust (Decety, 1996; Fadiga et al., 1999; Grèzes & Decety, 2001; Munzert et al., 2009). Furthermore, Pascual-Leone et al. (1995) demonstrated that physical and imagined practice of a one-handed piano exercise led to similar adaptations to the motor system. Therefore, a motor-priming account of these data would seem likely to be involved to some extent. Further work that separates the contribution of action representations and visual attention in action cognition is encouraged.

4.3. Implications for action cognition

Although our data show a similar interference effect with imagery as previously demonstrated with observation, these two methods of action representation hold distinct properties. Observation of another person's action is solely dependent on an external stimulus (another person), whilst imagery is self-generated. These contrasting characteristics are important for theories of how observation and imagery function in action cognition.

It has been suggested that engaging common motor structures between observation and execution helps to understand (Rizzolatti & Craighero, 2004; Rizzolatti et al., 2001) and predict other people's actions (Prinz, 1997; Wilson & Knoblich, 2005). To this end, a plausible mechanistic account of how intentions could be inferred from observed actions has been put forward (Kilner et al., 2007a,b). Kilner and colleagues posit that through reciprocal connections the mirror neuron system (IFG and IPL) and superior temporal sulcus (STS) function in a hierarchical manner to "tune" the motor system. In a similar fashion, imagery may perform a related role in understanding other people's actions. Simulation of movement, through imagery, may help to "tune" the motor system to respond more efficiently when observing actions (i.e., inferring the most likely intention of another person). The current study suggests that imagery can prime the motor system, and the extant neuroimaging literature suggests that the most likely neural substrates of this are IFG, IPL, SMA and CMA. On the basis of predictive-encoding as outlined by Kilner, Friston, and Frith (2007a,b), motor-priming through imagery may also minimise the prediction error in the higher-level components of the mirror neuron system: IFG and IPL. Action imagery would refine the information transfer between these higher-level components using "pretend" or imaginary actions as inputs instead of observed actions. As a consequence, during action observation, these higher-level components may process visual input from STS more efficiently in order to arrive at the most likely intention underlying an observed action.

This proposed function of imagery is appealing because it adds an additional level of flexibility to action understanding, which observation does not. Imagery permits motor simulations to be run in a reflective or recreative manner (Currie & Ravenscroft, 2002). That is, at any point in time one can imagine themselves or somebody else performing a previously performed or future action (Buckner & Carroll, 2007). Observation, on the other hand, only permits reflexive simulations in real time; an external stimulus must be present to observe and process. In both cases, however, it is plausible that observation and imagery may serve a similar purpose in action cognition: to minimise the prediction error in all or part of the mirror system in order to arrive at the most likely action intention of other people. Although the current work shows that imagery can prime execution, in order to make stronger claims

regarding imagery's influence on action understanding, other empirical work is necessary to show that imagery can directly influence the perception of action.

In the present paper we used a motor-priming paradigm to demonstrate for the first time that imagining a different action to that which is performed can interfere with the initiation of action production. Based on neuroimaging literature, we suggest that the most likely neural substrates for this interference effect are brain regions that respond during both imagery and execution of actions, such as IFG, IPL, SMA and CMA. These findings affirm the hypothesis that representing an action through imagery can prime the motor system by engaging similar neural processes as those used in execution (Jeannerod, 1994; Prinz, 1997).

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