Neuropsychologia 47 (2009) 786–795

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

The role of selective attention in matching observed and executed actions

Trevor T.-J. Chong[a,b,*], Ross Cunnington[c], Mark A. Williams[b], Jason B. Mattingley[c]

[a] *St Vincent's Hospital Melbourne, Fitzroy, Victoria 3065, Australia*
[b] *Macquarie Centre for Cognitive Science, Macquarie University, Sydney, NSW 2019, Australia*
[c] *Queensland Brain Institute & School of Psychology, The University of Queensland, St Lucia, Queensland 4072, Australia*

ARTICLE INFO

Article history:
Received 30 June 2008
Received in revised form
18 November 2008
Accepted 3 December 2008
Available online 13 December 2008

Keywords:
Action observation
Automatic imitation
Visuomotor priming
Mirror neuron system
Attention

ABSTRACT

Substantial evidence suggests that observed actions can engage their corresponding motor representations within the observer. It is currently believed that this process of observation–execution matching occurs relatively automatically, without the need for top-down control. In this study we tested the susceptibility of the observation–execution matching process to selective attention. We used a Go/NoGo paradigm to investigate the phenomenon of 'automatic imitation', in which participants are faster to initiate a hand movement that is congruent with a concurrently observed action, relative to one that is incongruent. First, we replicated previous findings of automatic imitation, and excluded the possibility that spatial compatibility effects might explain these results (Experiment 1). We then presented participants with the same goal-directed actions while directing their attention to an imperative stimulus that spatially overlapped, but was distinct from, the observed actions (Experiment 2). Crucially, automatic imitation no longer occurred when participants directed their attention away from the displayed actions and towards the spatially overlapping stimulus. In a final experiment, we examined whether the automatic imitation of grasp persists when participants attend to an irrelevant feature of the observed action, such as whether it is performed by a left or right hand (Experiment 3). Here we found that automatic imitation is contingent on participants attending to the feature of the observed hand that was relevant to their responses. Together these findings demonstrate the importance of selective mechanisms in the filtering of task-irrelevant actions, and indicate a role for top-down control in limiting the motoric simulation of observed actions.

1. Introduction

The notion that actions are intrinsically linked to perception is not new (Darwin, 1872/1965; James, 1890). Classical theorists noted that observers are prone to mentally simulating and imitating the actions of others (Carpenter, 1874; Chevreul, 1833; James, 1890; Lotze, 1852; Smith, 1759/1976). Darwin (1872/1965), for example, noted that spectators at leaping matches move their own feet as if imitating the athletes, and argued that man has a 'strong tendency to imitation, independently of the conscious will.' More recently, it has been shown that humans have a tendency to unconsciously and non-strategically mimic the bodily postures (Chartrand & Bargh, 1999), facial expressions (Dimberg, 1982; Vaughan & Lanzetta, 1980) or gross arm movements of other individuals (Kilner, Paulignan, & Blakemore, 2003). Furthermore, human neuroimaging studies have indicated that the process by which an observed action is transformed into its motor equivalent is mediated by the mirror neuron system—a network of parietal and premotor areas that respond both to the observation and execution of action (Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Dinstein, Gardner, Jazayeri, & Heeger, 2008; Grezes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 1999, 2001; Koski, Wohlschläger, Bekkering, Woods, & Dubeau, 2002; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Matelli et al., 1996).

It has been suggested that perceiving an action activates the corresponding motor representations within the observer automatically and without conscious effort (Buccino et al., 2001; Coricelli, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese & Metzinger, 2003; Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Matelli et al., 1996; Wilson & Knoblich, 2005). Evidence in favor of this proposal comes from studies that have recorded motor-evoked potentials (MEPs) during the passive observation of action, and which have shown increases in motor excitability specific to the muscles involved in performing those actions (Fadiga, Craighero, & Olivier, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). In addition, electroencephalography (EEG) and magnetoencephalography (MEG) studies indicate that the passive observation and active execution of action have similar effects on rhythmic oscillations originating from central regions of the brain (the mu and 20 Hz

---

[*] Corresponding author at: St Vincent's Hospital Melbourne, Fitzroy, Victoria 3065, Australia.
E-mail address: trevor.chong@svhm.org.au (T.T.-J. Chong).

0028-3932/$ – see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neuropsychologia.2008.12.008

rhythms, respectively) (Cochin, Barthelemy, Roux, & Martineau, 1999; Hari et al., 1998).

Behaviorally, a consistent finding in favor of the automaticity hypothesis arises from studies of so-called ‘automatic imitation’. This is the observation that participants are typically faster to execute an action that is congruent with one that is concurrently observed, relative to one that is incongruent (Brass, Bekkering, & Prinz, 2001a; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Heyes, Bird, Johnson, & Haggard, 2005; Press, Bird, Flach, & Heyes, 2005; Press, Gillmeister, & Heyes, 2006; Stürmer, Aschersleben, & Prinz, 2000; Vogt, Taylor, & Hopkins, 2003). Importantly, this effect is found even when the observed action is entirely irrelevant to participants' responses. Many studies on automatic imitation have utilized simple intransitive actions, such as a lifting/tapping movement of a finger, or an opening/closing movement of the hand (Brass et al., 2000; Brass, Bekkering et al., 2001; Heyes et al., 2005; Press et al., 2005, 2006; Stürmer et al., 2000). By comparison, fewer studies have examined the automatic imitation effect with more naturalistic, goal-directed movements, such as reach-to-grasp hand actions (Craighero et al., 2002; Vogt et al., 2003).

A representative example of an automatic imitation paradigm with goal-directed hand actions is the Go/NoGo task used by Craighero et al. (2002). In this paradigm, right-handed participants were trained to perform a precision grasp towards a clockwise- or counterclockwise-oriented bar that was positioned out of sight. Participants performed these movements in response to a ‘Go’ signal that was either the mirror image of their right hand in its final position or the mirror image of the right hand in the alternate end position. As predicted, reaction times were faster during the observation of congruent relative to incongruent hand postures. Furthermore, this congruency effect persisted even when the end-positions of the hands were similar but rotated rightwards by 90°, which the authors argued excluded the possibility that their results were caused by mere spatial compatibility (i.e., by simple matching of the end positions of the fingers and thumb to the imperative stimulus). In a subsequent study, Vogt et al. (2003) extended the findings of Craighero et al. (2002) in a simple reaction-time task. In this study, participants grasped a vertical or horizontal rod that was occluded from sight, in response to the appearance of any hand stimulus whatsoever, which could have been either congruent or incongruent with the executed action. The authors found that the automatic imitation of goal-directed actions persists even when no visual discrimination of the target stimulus is required.

Although such congruency effects suggest an underlying automaticity to the observation–execution matching process, the extent of this automaticity remains unclear. The traditional distinction between automatic and controlled processes is that the former are triggered involuntarily and do not require attention for their execution (Bargh, 1992; Cohen, Dunbar, & McClelland, 1990; Hasher & Zacks, 1979; Posner, 1978). A corollary of this definition is that automatic processes do not draw on general cognitive resources, and thus do not interfere with, nor are they subject to interference from, other concurrent perceptual or cognitive demands. Consequently, several such processes can operate in parallel in the absence of capacity limitations (Pashler, 1998). If the automaticity of the visuomotor transformation process is strong, an observed action should be processed independently of whether that action is selectively attended.

Crucially, however, previous experiments have not explicitly manipulated the allocation of attentional resources during the processing of an observed gesture. Thus, the role of selective mechanisms in the observation–execution matching process is uncertain. For example, some studies have required participants to perform a simple finger movement (e.g., lifting or tapping a finger) in response to a symbolic cue (such as a numeric prime which denotes the finger to be moved) or a spatial cue (such as a cross on an image of the finger to be moved) (Bertenthal, Longo, & Kosobud, 2006; Brass et al., 2000). While participants attended to these cues, they were concurrently presented with the image of a congruent or incongruent finger movement. The typical finding is that automatic imitation occurs even when participants' attention is directed towards the secondary symbolic or spatial cue, and away from the observed finger movement. Superficially, this would appear to be evidence in favor of automaticity of the visuomotor transformation process. However, such findings usually arise in the presence of attentionally salient actions (e.g., those with a component of motion). Because moving stimuli may act as powerful exogenous cues (Posner & Cohen, 1984), it is unclear whether these apparent congruency effects arise as a result of some inherent automaticity to the visuomotor transformation process, or simply due to the involuntary capture of attention by the moving (albeit task-irrelevant) actions.

It has also been shown that automatic imitation persists when participants attend to a feature of an observed action that is orthogonal to the required response (e.g., attending to the *color* of a hand to execute the appropriate hand *movement*, Stürmer et al., 2000). Often, however, the orthogonal discrimination imposes a low processing load on cognitive resources. Previous studies on selective attention have shown that such low processing loads can allow attentional resources to ‘spill over’ to the processing of other irrelevant features of a stimulus (Lavie, 1995, 2000). In the present context, the consequence would have been to allow attentional resources not already consumed by the response-orthogonal discrimination to be engaged in processing the response-relevant feature of the observed action.

To summarize, the effect of selective attention on visuomotor transformations of observed actions remains unclear. Nevertheless, there are strong *a priori* reasons for supposing that the processing of observed actions should be susceptible to top-down modulation. In the natural environment, for example, we are typically confronted with several actions and gestures simultaneously, of which only a fraction are behaviorally relevant. Selective mechanisms should be critical in enhancing the processing of these actions, while suppressing those that are irrelevant or otherwise distracting. In fact, the importance of selective attention in processing observed actions was demonstrated in a recent functional magnetic resonance imaging (fMRI) study, which found that increasing the attentional load of a secondary task suppressed activity within left inferior frontal gyrus (IFG, BA 45; Chong, Williams, Cunnington, & Mattingley, 2008)–an area that has previously been implicated in the action observation network.

In addition to the neuroimaging study of Chong, Williams et al., 2008, emerging behavioral data have provided evidence that spatial attention may be important in the perception of body parts in general. Bach, Peatfield, and Tipper (2007) required participants to respond to the color of a target disc by pressing a corresponding button with either their foot or their finger. The authors' manipulation was to superimpose the colored targets on either the foot or hand on a whole-body display. They found that reaction times were faster when the attended body part (e.g., the hand) matched the corresponding effector (e.g., a button press with one's finger). This result shows that attending to a body part non-specifically primes motor responses involving that particular effector. However, the authors also found that attending to a neutral body part (e.g., the head) completely suppressed this visuomotor priming effect. This result emphasizes the role of spatial attention in action observation, by showing that only those body parts that appear within the spotlight of attention get processed. However, it is currently uncertain whether selective processes continue to be important when observed actions can be specifically mapped onto participants' own motor responses (i.e., in automatic imitation). Furthermore, the question remains as to whether selective mechanisms are capable of suppressing the visuomotor transformation of observed actions even when those actions appear at a spatially attended location.

The overarching goal of this study was to use a single experimental paradigm to investigate the effect of selective attention on the process of observation–execution matching. We used a Go/NoGo paradigm that was modified from that of Craighero et al. (2002). Specifically, participants were required to grasp a vertically oriented rod with either a *precision* or *whole-hand* grasp in response to a congruent or incongruent 'Go' signal. The specific features of our design were biologically motivated and intended to build on previous studies of automatic imitation. First, we chose to examine goal-directed actions, as mirror neurons show preferential activity for goal-directed actions over meaningless gestures (Rizzolatti, Fogassi, & Gallese, 2001). Second, instead of having participants perform identical grasps to a target object that differed only in its orientation (Craighero et al., 2002; Vogt et al., 2003), we fixed the target object in a single position and varied the reach-to-grasp action to be performed. We chose to vary the congruency of the action as a function of grasp based on extensive macaque data which demonstrate a sensitivity of mirror neurons to end-effector configurations (e.g., grasping, tearing, and manipulating) (Gallese et al., 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Third, we used images of stationary hand actions rather than moving hand actions, to examine the effects of task demands independent of stimulus salience. Lastly, our target object was always in full view of participants. The two previous studies that used transitive gestures occluded participants' view of the object (Craighero et al., 2002; Vogt et al., 2003), which might be less naturalistic than situations encountered in everyday life. In this study, we chose to present the target object in full view of participants based on empirical evidence showing that grasping movements towards an occluded object rely on the ventral visual pathway, and are qualitatively different from those towards a visible object, which rely on the dorsal pathway (Cant, Westwood, Valyear, & Goodale, 2005; Goodale, Jakobson, & Keillor, 1994; Hu & Goodale, 2000; Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999; Westwood & Goodale, 2003). It thus remains to be determined whether automatic imitation of goal-directed actions occurs only for actions that are memory-guided, or whether this automaticity occurs as part of a more general visuomotor priming mechanism (c.f. Cant et al., 2005).

In Experiment 1, our primary aim was to replicate the finding of automatic imitation with our new stimuli, prior to investigating the critical issue of the role of selective attention in the observation–execution matching process. Experiment 2 then assessed the extent to which an unattended hand could give rise to automatic imitation. In this experiment, participants selected their grasp while directing their attention to a secondary stimulus at fixation, which was overlaid upon a task-irrelevant hand action. Finally, Experiment 3 examined whether automatic imitation can be modulated by having participants attend to a feature of the observed hand that was orthogonal to the response-relevant dimension. Participants in this experiment were required to select their grasp on the basis of the laterality of the target (a left or right hand)—a cognitively demanding discrimination that aimed to reduce the attentional resources available to participants for processing the grasp configuration of the hand. Importantly, Experiments 2 and 3 held constant the low-level properties of the displays, and manipulated only the feature of each stimulus that was attended.

2. Experiment 1

Based on previous findings of automatic imitation, our prediction was that the appearance of a hand action that matched the final posture of the executed movement should facilitate participants' reaction times, relative to the observation of incongruent gestures. This finding would be further evidence in favor of a visuomotor coupling between a perceived stimulus and a subsequent action.

In this initial experiment, we also aimed to exclude the possibility that automatic imitation is driven simply by a spatial compatibility effect (e.g., by participants matching the position of their index finger to the location of the index finger in the display). As previously mentioned, Craighero et al. (2002) investigated this possibility by presenting participants with two different sets of stimuli: in one set, stimuli were mirror-images of the clockwise or counterclockwise grasps that participants had to perform; in the other, stimuli were the same images but rotated by 90° rightwards. The authors found identical automatic imitation effects for both stimulus sets. They concluded that such effects were unlikely to be caused by spatial compatibility alone, and were more likely to be due to sophisticated visuomotor-matching mechanisms. It should be noted, however, that in both the rotated and non-rotated sets of stimuli, the relative positions of the index finger and thumb in the congruent condition matched those of participants' own end positions for the grasps they performed. Thus, one cannot completely exclude the possibility of a spatial compatibility effect in accounting for the automatic imitation found by Craighero et al. (2002). In the present study, we reasoned that, if automatic imitation is secondary to a spatial compatibility effect, it should only be present during the observation of a mirror image (left) hand, and not during an anatomically symmetric (right) hand, with the relative positions of fingers and thumb reversed. We therefore presented participants with images of both left and right hands to investigate this hypothesis.

Finally, automatic imitation is usually described in relation to reaction times to initiate a movement. It is possible, however, that the effects of visuomotor priming may extend to the profile of the reach-to-grasp movement itself. We therefore measured two distinct movement parameters: the time to commence each movement (Initiation time) and the time between commencing the movement and grasping the target object (Transport time).

2.1. *Method*

2.1.1. *Participants*

Sixteen students from the University of Melbourne gave their informed consent to participate in this study (average age 22.1 years; S.D. 6.41 years; 12 females). All participants were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal vision. No participants reported a history of neurological illness. All of the experiments reported in this paper were approved by the ethics committee at the University of Melbourne, Australia, and were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.1.2. *Stimuli and apparatus*

Participants were tested individually in a dimly lit room. Participants commenced each trial by depressing a button located immediately in front of them (Fig. 1). At the onset of a target stimulus, they performed a reach-to-grasp movement towards a vertically oriented rod located approximately 30 cm in front of the body midline. The rod had a diameter of 3.3 cm and height of 14.3 cm, and was supported by a base of diameter 12 cm and height 1.2 cm. The rod contained a force-sensitive resistor along its right edge that was used to measure the transport time between releasing the response button and grasping the target object.

Stimuli were stationary images of a left or right hand viewed from an allocentric perspective against a black background (Fig. 2a). Stimuli of the right hand were derived by horizontally flipping images of the left hand. The hand assumed one of two prehensive postures—a precision grip (with index finger and thumb outstretched) or a whole-hand power grip (with four fingers and thumb outstretched). The dimensions of the hands were life-sized and subtended a viewing angle of ∼9.5° horizontally and ∼12.4° vertically, as viewed from a distance of 60 cm. Stimuli were presented at the center of a CRT monitor at a screen resolution of 1024 × 768 and refresh rate of 85 Hz. Stimulus delivery and data recording were controlled with Presentation software (Neurobehavioral Systems; http://www.neurobs.com), which was run on an Intel Pentium IV 3.2 GHz computer with 1024 Mb of RAM and a 256 Mb AGP NVidia video card.

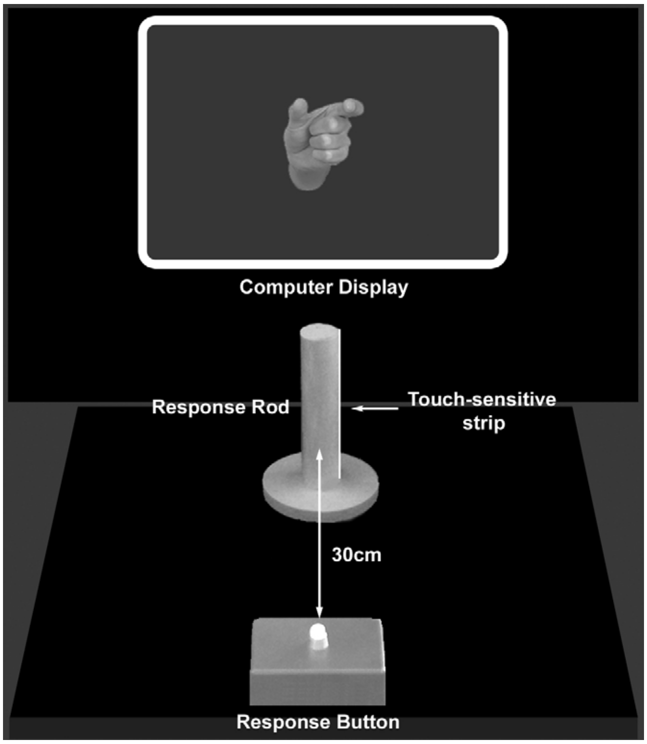

Fig. 1. Visual display and response rod used in Experiments 1–3, as viewed from the participants' perspective. Stimuli and apparatus were arranged against a black, featureless background. Participants commenced each trial by holding down a central button with their right middle finger. In the event of a target 'Go' stimulus, participants executed a reach-to-grasp movement towards a vertically oriented rod. A touch-sensitive strip located on the right edge of the rod detected participants' responses. Two movement parameters were measured: the time prior to movement selection and initiation (Initiation time) and the time required for movement completion (Transport time).

2.1.3. Procedure

The experiment utilized a Go/NoGo paradigm (Fig. 2c), in which the 'Go' signal corresponded to the particular grip configuration of the hand image and alternated between blocks. Thus, in separate blocks, participants responded only to the precision grip or only to the whole-hand grip presented in the display. In order to commence each trial, participants held down the start button located immediately in front of them using the middle finger of their right hand. They were instructed to keep this button depressed until the onset of a 'Go' stimulus. After depressing the button, an instruction appeared in the center of the display regarding the specific movement that participants were to execute in the event of a 'Go' trial. This instruction was presented as a numeric display—the number '1' instructed participants to perform a precision (one-finger) grip, and the number '4' represented a whole-hand (four-finger) grip. Thus, the grasps that participants themselves performed were either congruent or incongruent with the hand images that were presented, but the identity of the hand images were entirely irrelevant to the type of grasp that participants performed. The numeric instruction was displayed for 1.5 s, and was followed by a random fixation period of between 1 and 2 s to prevent anticipations. At the conclusion of the fixation period, the imperative target stimulus – a left or right hand in a precision or whole-hand grip – appeared. In the event of a 'Go' stimulus, participants released the button and executed a reach-to-grasp movement towards the target object. Stimuli were present on the display until participants completed their grasp by activating the force-sensitive resistor. In the event of a 'NoGo' trial, stimuli remained present for 1.5 s prior to the onset of the next trial.

Participants completed 256 trials across four separate blocks, which were counterbalanced according to the 'Go' stimulus in an ABBA design. Prior to each block, participants completed a practice block of 20 trials, which were not analyzed. 'Go' and 'NoGo' trials were presented randomly but with equal frequency within each block. For all trials, we measured the time between stimulus presentation and movement onset (corresponding to release of the start button; 'initiation time'), and the time between movement onset and the completion of the movement (corresponding to activation of the force-sensitive resistor; 'transport time'). In addition, an experimenter seated out of sight behind each participant monitored their responses for accuracy, and their responses were verified offline through videotaped recordings of participants' grasps.

2.2. Results

Trials in which participants committed an error were eliminated from the main analysis. These included trials in which participants incorrectly initiated a movement in response to a 'NoGo' trial, or performed an incorrect grasp during a 'Go' trial. To minimize the effect of outliers on the main analysis, we excluded reaction times that were greater than three standard deviations from the conditional means of each participant.

Data were analyzed with a two-way repeated measures analysis of variance (ANOVA) on the factors of Hand Image Laterality (Left vs. Right) and Congruency (Congruent vs. Incongruent). Separate ANOVAs were conducted for mean initiation times and mean transport times. The ANOVA on mean initiation times revealed a significant main effect of Congruency ($F_{(1,15)} = 11.241$, $p < 0.005$); responses were faster for Congruent (*M* 410 ms, S.E. 8.80) than for Incongruent trials (*M* 434 ms, S.E. 9.95) (Fig. 3). However, neither the main effect of Hand Image Laterality ($F_{(1,15)} = 0.167$, n.s.) nor its interaction with Congruency ($F_{(1,15)} = 0.442$, n.s.) were significant. The ANOVA on mean transport times did not reveal any significant effects of Hand Image Laterality ($F_{(1,15)} = 0.751$, n.s.), Congruency ($F_{(1,15)} = 0.970$, n.s.) or their interaction ($F_{(1,15)} = 0.048$, n.s.).

The overall mean error rate across participants was 2.7%. Errors included trials in which participants incorrectly executed a 'Go' response to a 'NoGo' stimulus (false starts, 4.4% of 'NoGo' trials), and trials in which participants performed an incorrect grasp to the target object (incorrect grasps, 0.9% of all 'Go' trials). Separate two-way repeated measures ANOVAs on the factors of Hand Image Laterality and Congruency were conducted for both types of error. These ANOVAs revealed no significant main effects or interactions. It is therefore unlikely that the initiation time effects can be attributed to a speed-accuracy tradeoff.

2.3. Discussion

As predicted, participants were faster to initiate their responses to Congruent relative to Incongruent stimuli. This outcome replicates previous findings of automatic imitation in the behavioral literature (Bertenthal et al., 2006; Brass et al., 2000; Brass, Bekkering et al., 2001; Craighero et al., 2002; Heyes et al., 2005; Press et al., 2005, 2006; Stürmer et al., 2000; Vogt et al., 2003), and excludes the possibility of a speed-accuracy tradeoff in accounting for the results. In addition, we show that the automatic imitation of goal-directed actions persists even when motion salience is controlled with the use of stationary stimuli. Furthermore, because these congruency effects are independent of Hand Image Laterality, it is more likely that they are caused by a higher level representation of the grasp itself rather than mere spatial compatibility. This finding is consistent with the data from Craighero et al. (2002) regarding spatial compatibility, but we extend these previous results by showing that the automatic imitation effect persists even when the postures of the hands are mirror-reversed images of participants' end hand positions.

Although the principal aim of Experiment 1 was to replicate the automatic imitation effect, our findings also extend previous studies by showing that automatic imitation occurs for visually guided grasping movements. In the only two studies on transitive actions performed thus far, Craighero et al. (2002) and Vogt et al. (2003) required participants to grasp an occluded object. There is considerable evidence that grasping an occluded object relies on planning from object memory in the ventral visual pathway rather than direct visual input via the dorsal route (Cant et al., 2005; Goodale et al., 1994; Hu & Goodale, 2000; Milner et al., 1999; Westwood & Goodale, 2003). The ventral pathway is exquisitely sensitive to priming effects, and it is therefore not surprising that automatic imitation is seen during actions towards an occluded

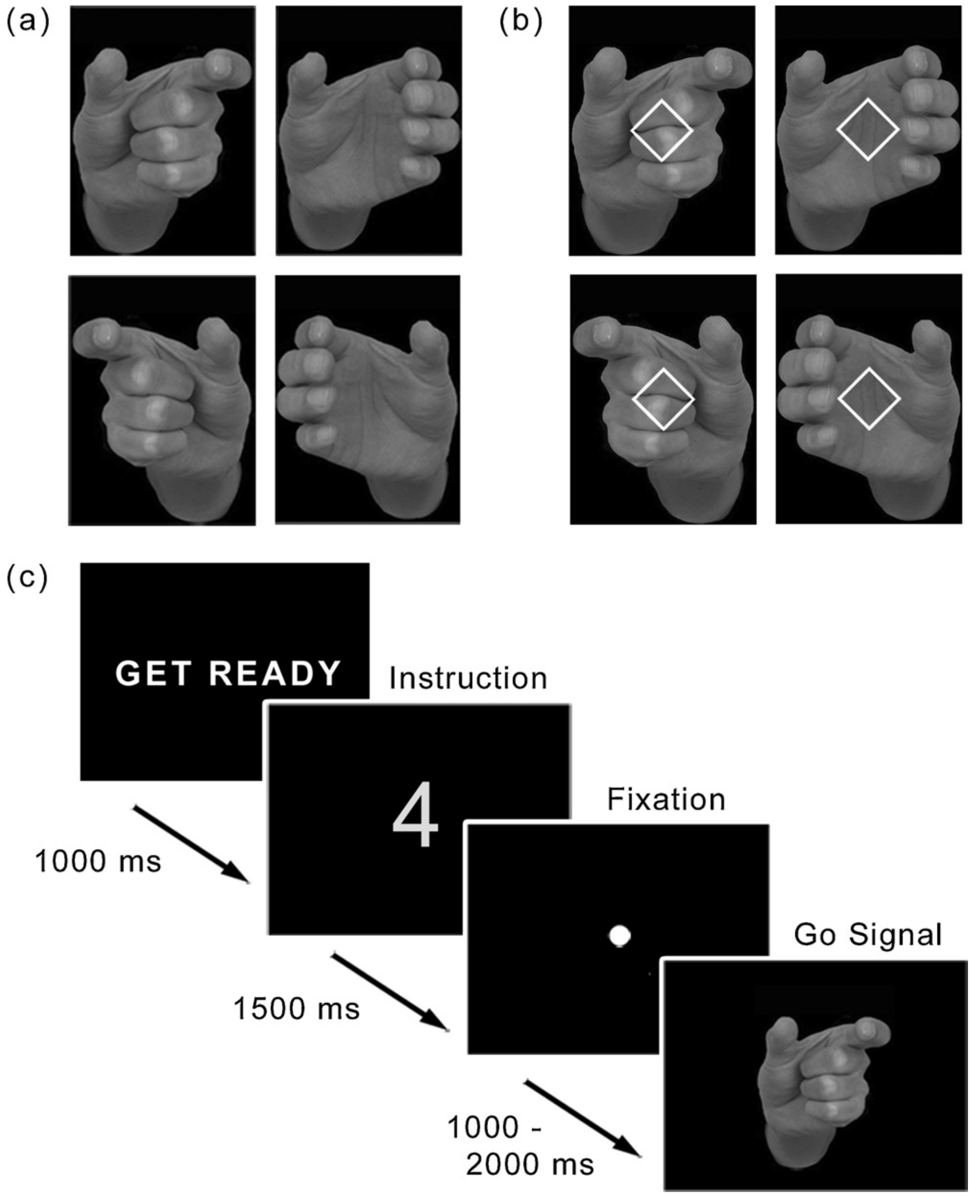

Fig. 2. Examples of the stimuli used in Experiments 1–3, and sequence of events in a typical trial. (a) The four hand actions used in Experiments 1 and 3. These were images of left or right hands in the posture of a precision or a whole-hand grasp. These actions were presented against a black background and viewed from an allocentric perspective. Images of right hands were mirror-reversed images of left hands. (b) Sample stimuli used in Experiment 2. As in Experiment 1, hand actions were images of left or right hands in the posture of a precision or whole-hand grasp. Superimposed on each hand action was a diamond-shaped outline, which was colored red or blue. (c) In each trial, participants first received a numerical instruction regarding the type of action they were to perform in the event of a target 'Go' signal ('1' = precision grip and '4' = whole-hand grip). This was followed by a variable fixation period of 1–2 s, after which the target hand action appeared on the display. Stimuli were present until the reach-to-grasp movement was completed in a 'Go' trial, or after a period of 1.5 s in the event of a 'NoGo' trial.

object. In contrast, visually guided actions engage a different set of visual mechanisms that are dedicated to transforming retinal information into action in real-time. The question of whether automatic imitation also occurs towards visible objects was therefore an empirical one. Our finding that congruency effects persist even for visually guided grasps suggests that the dorsal stream areas involved in vision-for-action are also susceptible to task-irrelevant motor primes.

Finally, it is worth noting that automatic imitation occurred only for initiation time and not for transport time. One interpretation of this finding is that the effect of an observed action on action execution occurs at relatively early stages of response selection, and is no longer evident once the movement has been initiated. It is possible that our use of stationary stimuli may have contributed to this greater congruency effect for response selection relative to action execution. In particular, these stimuli had to be processed and recognized prior to movement execution, and they became irrelevant once the movement had been initiated. We might speculate that moving images may be more likely to give rise to congruency effects during the transport phase of the movement, as they contain greater information about the kinematics of the action, and may also continue to influence that action once it has been initiated. Theoretically, it would be interesting to examine the effects of moving stimuli in a similar automatic imitation paradigm, although such effects would have to be interpreted cautiously given the attentional salience of any moving stimulus. The absence of a congruency effect in the measure of transport time is discussed further in Section 5.

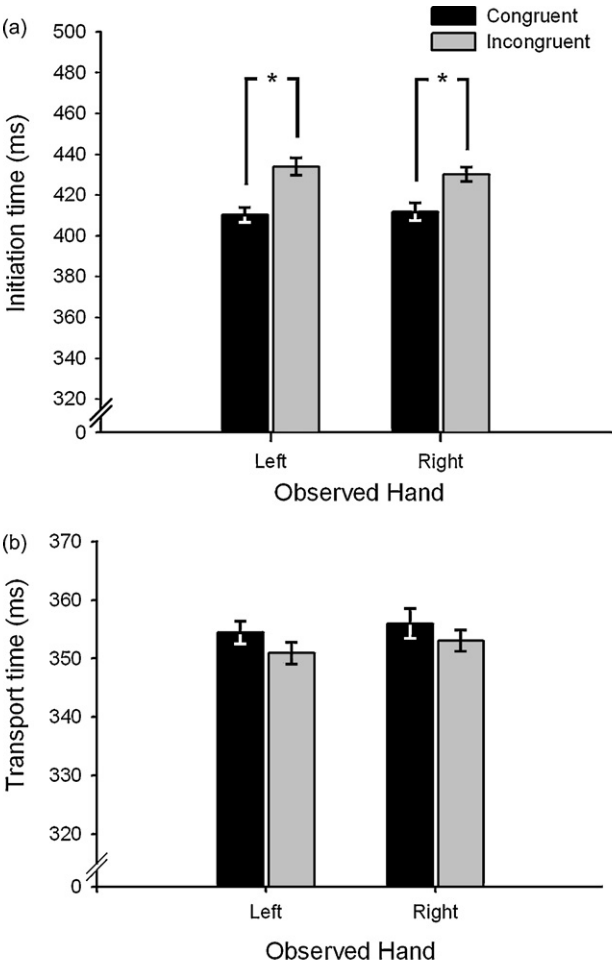

Fig. 3. Data from Experiment 1. Graphs of (a) mean initiation time and (b) transport time for the execution of Congruent and Incongruent hand actions, plotted separately for the observation of left and right hands. Significant congruency effects were found for initiation time during the observation of both left and right hands. Error bars indicate +1 within-subjects S.E. $^{*}p < 0.005$.

3. Experiment 2

Having replicated previous findings of automatic imitation, Experiment 2 investigated whether these congruency effects persist independently of the task-relevance of the observed stimulus. If an observed action is processed automatically, then directing participants' attention to a secondary stimulus should not significantly alter the congruency effect induced by the observed hand. In Experiment 2, half the blocks were identical to those in Experiment 1 (Attend Grasp), and required participants to attend to the grip configuration of each hand for the relevant 'Go' signal. In the remaining half of the blocks, participants' attended to a diamond-shaped outline that spatially overlapped the center of the observed hand, the color of which formed the critical 'Go' signal (Attend Color; Fig. 2b). Importantly, identical stimuli were used in both the Attend Grasp and Attend Color tasks; the only difference between the two conditions was in the feature of the display that was task-relevant.

3.1. Method

3.1.1. Participants

A new group of 16 right-handed, neurologically healthy participants gave their informed consent to participate in this study (average age 21.6 years; S.D. 6.30 years; 12 females). All participants were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal vision. No participants reported a history of neurological illness.

3.1.2. Stimuli

Stimuli of hand images were identical to those used in Experiment 1. However, superimposed on each hand stimulus was a diamond-shaped figure that was colored red or blue (Fig. 2b). The diamond frame subtended a viewing angle of ∼3.3°, and spatially overlapped the center of each hand. Notably, the part of the hand which the diamond overlapped contained information that would be important in discriminating the posture of the observed hand (an open or closed hand).

3.1.3. Procedure

This experiment was conducted using the identical Go/NoGo paradigm as that used in Experiment 1. Two blocks were direct replications of Experiment 1 (Attend Grasp), in which participants attended to the grasp configuration (precision or whole-hand grip) as their 'Go' signal. In the remaining two blocks (Attend Color), the 'Go' stimulus was the color of the diamond outline, which was either red or blue. Importantly, the displays of hands and overlaid diamonds in the 'Attend Grasp' and 'Attend Color' blocks were identical; the blocks differed only in the stimulus dimension to which participants attended.

Prior to each block, participants were informed of the relevant 'Go' signal—a precision or whole-hand grip in the Attend Grasp blocks, and a red or blue diamond in the Attend Color blocks. 'Go' and 'NoGo' trials were presented equiprobably in each block, and the Attend Grasp and Attend Colour blocks were counterbalanced within participants in an ABBA sequence. All participants completed 256 trials and, prior to each experimental block, completed 20 practice trials, data from which were not analyzed.

3.2. Results

A two-way repeated measures ANOVA was conducted on the factors of Task (Attend Grasp vs. Attend Color) and Congruency (Congruent vs. Incongruent). Incorrect trials and outliers greater than three standard deviations from each participant's conditional mean were not analyzed.

The ANOVA on mean initiation time revealed a significant main effect of Task ($F_{(1,15)} = 76.728$, $p < 0.0001$), indicating that participants responded faster in the Attend Color task (*M* 393 ms, S.E. 12.7) than in the Attend Grasp task (*M* 444 ms, S.E. 13.1). There was also a significant main effect of Congruency ($F_{(1,15)} = 7.454$, $p < 0.05$), indicating that participants responded faster in the Congruent condition (*M* 412 ms, S.E. 11.8) than in the Incongruent condition (*M* 425 ms, S.E. 13.7). Most importantly, there was also a significant interaction between Task and Congruency ($F_{(1,15)} = 9.457$, $p < 0.01$). Simple main effect analyses (Bonferroni adjusted) of this interaction revealed an initiation time advantage for congruent over incongruent trials only for the Attend Grasp task (Congruent *M* 431 ms vs. Incongruent *M* 456 ms, $p < 0.005$), and not the Attend Color task (Congruent *M* 393 ms vs. Incongruent *M* 394 ms; n.s.) (Fig. 4). The ANOVA on mean transport time revealed no significant effects of Task, Congruency or their interaction ($F < 0.6$, n.s.).

The overall error rate in this experiment was 1.6%. Errors included trials in which participants incorrectly executed a 'Go' response to a 'NoGo' stimulus (false starts, 2.4%), and those in which they performed an incorrect grasp to the target object (incorrect grasps, 0.63%). The ANOVA on false starts revealed a significant main effect of Task ($F_{(1,15)} = 15.380$, $p < 0.001$), such that more reaches were incorrectly initiated during the Attend Grasp task (*M* 1.05%, S.E. 0.238) than in the Attend Color task (*M* 0.17%, S.E. 0.0797). The main effect of Congruency ($F_{(1,15)} = 2.500$, n.s.) and the interaction between Task and Congruency ($F_{(1,15)} = 0.894$, n.s.) were not significant. The ANOVA on incorrect grasps did not reveal any significant main effects or interactions.

3.3. Discussion

The Attend Grasp task replicated the automatic imitation effect found in Experiment 1, and again showed that these effects are manifest in initiation rather than transport times. Critically, however, the data also demonstrate that automatic imitation is contingent on the task-relevance of the observed action. Specifically, the congruency effects were no longer significant when participants directed their attention away from the background hand stimulus and

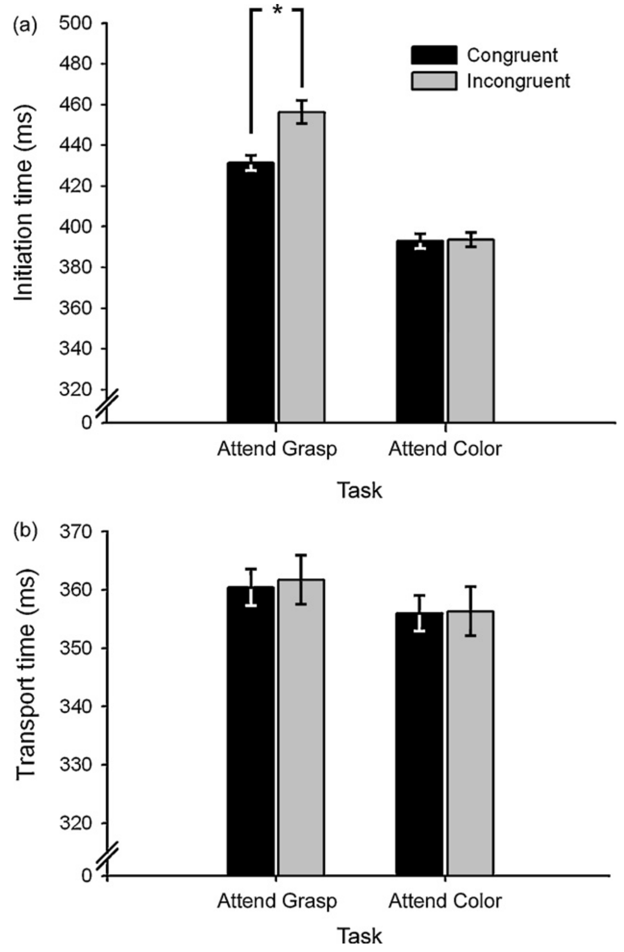

Fig. 4. Data from Experiment 2. Graphs of (a) mean initiation time and (b) transport time for the execution of Congruent and Incongruent hand actions, plotted separately for the Attend Grasp and Attend Color tasks. There was a significant congruency effect in initiation time for the Attend Grasp task, but not the Attend Color task. Error bars indicate ±1 within-subjects S.E. $^{*}p < 0.005$.

towards the task-relevant diamond. Notably, this occurred despite the task being relatively undemanding (as reflected by the faster overall initiation times in the Attend Color relative to the Attend Grasp blocks). In addition, both the hand and colored diamond were presented at fixation, with the colored stimulus overlapping a part of the gesture that was important for participants to determine grip type (the opened or closed hand). The preliminary conclusion from Experiment 2, therefore, is that an observed gesture must be selectively attended for it to exert a measurable effect on the initiation of an executed action.

It should be noted that in this experiment participants either attended away from the hand stimulus entirely (in the Attend Color condition), or towards a specific feature of the hand that could be mapped onto their own responses (in the Attend Grasp condition). Thus, a question that remains is whether it is sufficient for participants to attend to *any* feature of the observed action, or whether they must attend to a *response-relevant* feature of that action, for automatic imitation to occur. Experiment 3 aimed to distinguish between these possibilities.

4. Experiment 3

In Experiment 3, participants were presented with the identical stimuli as in Experiment 1 (i.e., left and right hands in the absence of the diamond outline). In half the blocks, participants attended to the grip configuration of the hand in order to derive the 'Go' signal. These blocks were therefore identical to those used in Experiment 1 and the Attend Grasp task of Experiment 2. In the remaining half of the blocks (Attend Laterality), the grip configuration was irrelevant, and the 'Go' signal for participants was determined by the laterality of the hand (i.e., whether the stimulus shown was a left or right hand). Importantly, discriminating a hand's laterality requires a judgment that is unrelated to discriminating its grasp type. Furthermore, this type of orthogonal cue imposes a greater cognitive load than that used in previous studies on automatic imitation (e.g., discrimination of a hand's color). By increasing the processing load imposed by the secondary task, we were able to limit the attentional resources available for processing of the response-relevant features of the action (i.e., its grasp).

4.1. *Method*

4.1.1. *Participants*

A further group of 20 participants from the University of Melbourne gave their informed consent to participate in this study (average age 22.4 years; S.D. 6.56; 18 females). None of these participants had participated in the earlier experiments. All participants were right handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and had normal or corrected-to-normal vision. No participants reported a history of neurological illness.

4.1.2. *Stimuli*

Stimuli were identical to those used in Experiment 1 (i.e., they comprised images of the precision and whole-hand grips without the superimposed diamond outline).

4.1.3. *Procedure*

The procedure was similar to that of Experiments 1 and 2. In half of the blocks (Attend Grasp), the decision to initiate a response was determined by the grasp configuration of the observed hand (i.e., a precision or whole-hand grip). In the remaining half of blocks (Attend Laterality), participants ignored the grasp configuration of the hand, and judged its laterality (i.e., whether it was a left or right hand) to determine whether a response was required.

4.2. *Results*

The analysis of Experiment 3 was similar to that of Experiment 2. A two-way repeated measures ANOVA was conducted on the factors of Task (Attend Grasp vs. Attend Laterality) and Congruency (Congruent vs. Incongruent). Invalid trials were eliminated as in Experiments 1 and 2. The ANOVA on mean initiation time revealed a significant main effect of Task ($F_{(1,15)} = 9.254$, $p < 0.01$), such that participants were faster to discriminate Grasp (*M* 450 ms, S.E. 16.7) than Laterality (*M* 477 ms, S.E. 21.4). This verifies the attentionally demanding nature of the Attend Laterality task. The main effect of Congruency was also significant ($F_{(1,15)} = 7.894$, $p < 0.05$), indicating that initiation times to Congruent trials (*M* 457 ms, S.E. 18.2) were faster than those to Incongruent trials (*M* 470 ms, S.E. 19.3). Importantly, however, the interaction between Task and Congruency was also significant ($F_{(1,15)} = 4.626$, $p < 0.05$). Simple main effect analyses (Bonferroni adjusted) of this interaction revealed a significant congruency effect for the Attend Grasp condition (Congruent *M* 437 ms vs. Incongruent *M* 462 ms, $p < 0.005$), but not for the Attend Laterality condition (Congruent *M* 478 ms vs. Incongruent *M* 477 ms, $p = 0.936$) (Fig. 5). The ANOVA on mean transport times revealed no significant main effects (Task, $F_{(1,15)} = 1.102$, n.s.; Congruency, $F_{(1,15)} = 0.050$, n.s.) or interactions ($F_{(1,15)} = 1.691$, n.s.).

The overall error rate was 3.0%. Errors included trials in which participants incorrectly executed a 'Go' response to a 'NoGo' stimulus (4.2%), and those in which they performed an incorrect grasp to the target object (1.8%). ANOVAs on these errors revealed no significant main effects or interactions, thus excluding a speed-accuracy tradeoff.

4.3. *Discussion*

The results from Experiment 3 indicate that attending to a specific feature of an action stimulus (such as its laterality) does not

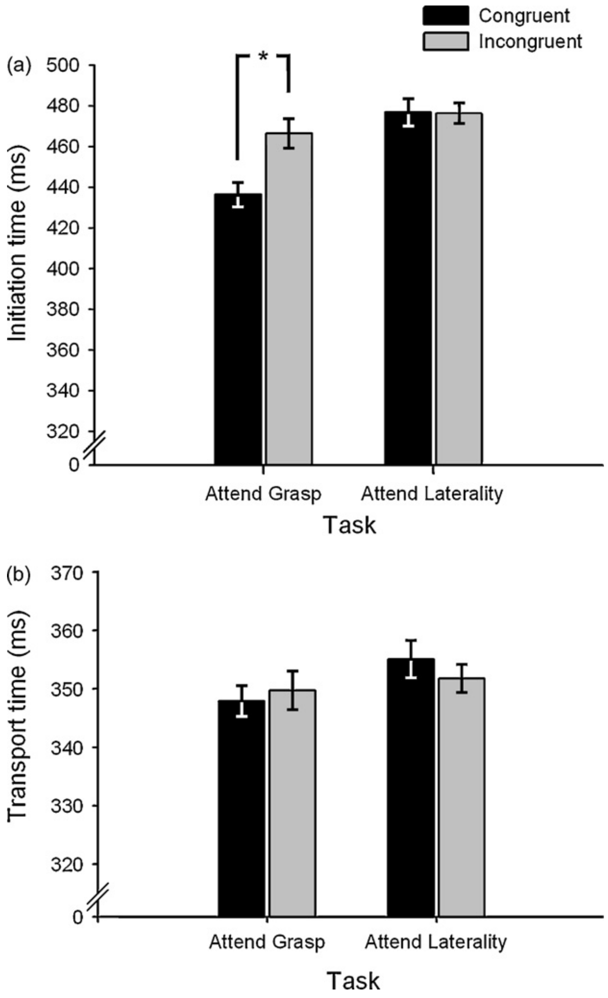

Fig. 5. Data from Experiment 3. Graphs of (a) mean initiation time and (b) transport time for the execution of Congruent and Incongruent hand actions, plotted separately for the Attend Grasp and Attend Laterality tasks. There was a significant congruency effect in initiation time for the Attend Grasp task, but not the Attend Laterality task. Error bars indicate ±1 within-subjects S.E. $^*p < 0.005$.

automatically lead to the processing of the entire action. Instead, the initiation of a grasp is only affected by the observed hand when participants attend to its grasp configuration, and not when they attend to a feature of the stimulus (its laterality) that is unrelated to the required response. Furthermore, by engaging participants in an orthogonal task that is relatively attentionally demanding (as suggested by the main effect of Task), we were able to limit the attentional resources that were available to process the grasp configuration of the hand. Together with the results from Experiment 2, these data indicate that automatic imitation is contingent on participants attending to a feature of the observed stimulus that is relevant to their response. The implications of these findings are discussed below.

5. General discussion

The present study investigated the role of selective processes in modulating the automatic imitation of goal-directed hand actions. Experiment 1 verified previous findings of automatic imitation by showing that the execution of reach-to-grasp actions is faster for congruent relative to incongruent movements. Importantly, we showed that this is not simply driven by a general spatial compatibility effect, and that the effect also occurs for visually guided grasps. Experiment 2 investigated the effect of directing attention towards an imperative stimulus which spatially overlapped, but was distinct from, the displayed actions. The critical finding was that automatic imitation no longer occurs when an observed gesture is task-irrelevant. Finally, Experiment 3 examined whether the automatic imitation of grasp can also be attenuated by directing attention towards a feature of the observed hand that is orthogonal to participants' responses. The results showed that attending to the laterality of the displayed hand did not lead to the automatic processing of its grasp configuration. Together, these findings argue against the proposal that the observation–execution matching process is automatic, and reveal the critical role of selective attention in the visuomotor transformation process.

Our findings accord with a recent behavioral study by Bach et al. (2007), who showed that spatial attention is necessary for an observed body site (e.g., an arm or a foot) to prime a button-press response involving the corresponding effector. The present study extends these recent findings in two important ways. First, we show that attention also plays a critical role during the specific imitation of an observed gesture. Second, we show that selective attention is capable of modulating the processing of task-irrelevant gestures, even when those gestures are spatially contained within the spotlight of attention. A strength of the present paradigm is that, in both Experiments 2 and 3, participants were always presented with identical stimuli, and foveated the identical regions of space within those stimuli, regardless of the task (Attend Grasp, Attend Color or Attend Laterality). By only manipulating the item to which participants attended, we were able to convincingly demonstrate the effect of selective attention in modulating the automatic imitation effect.

The Task × Congruency interactions in Experiments 2 and 3 demonstrate that the presence of a competing cognitive task may inhibit the visuomotor transformation of an observed action. This informs previous studies on automatic imitation. For example, automatic imitation has apparently been found even in simple reaction time studies, in which participants are not required explicitly to discriminate any feature of the displayed action, but simply to respond with a predetermined gesture (e.g., Heyes et al., 2005; Press et al., 2005, 2006; Vogt et al., 2003). However, because the processing of actions in these studies was not challenged by a secondary stimulus (c.f. Experiment 2) or cognitively demanding task (c.f. Experiment 3), greater resources would have been available to involuntarily match these actions with their motor equivalent. Our data suggest that, when cognitive resources are directed away from the action itself or are limited by a secondary task, few resources remain to facilitate the process of observation–execution matching (c.f. Lavie, 1995, 2000).

Furthermore, our findings demonstrate that stimulus salience plays an important role in automatic imitation. For example, previous studies have reported that the initiation of a motor response can be influenced by moving actions presented in the background, despite those actions being task-irrelevant (Bertenthal et al., 2006; Brass et al., 2000; Brass, Bekkering et al., 2001). However, motion can be a powerful cue which is capable of capturing exogenous attention (Posner & Cohen, 1984). Consequently, the involuntary processing of moving, task-irrelevant gestures in previous studies may have been driven by the visual salience of the stimuli, rather than by automaticity of the observation–execution matching process itself. Once motion salience is controlled through the use of stationary stimuli (as in Experiment 2), it seems task-irrelevant actions can be successfully filtered, and cease to undergo visuomotor transformation.

A further finding of the present study is that the processing of a critical feature of an observed action (here, its grasp) occurs only when attention is directed towards that feature. This finding may appear inconsistent with previous studies which have shown that attending to the color of a hand nevertheless results in congruency effects related to the hand's posture (e.g., Stürmer et al., 2000). However, in this instance, the finding of automatic imitation may have been due to the nature of the required discrimination. In particular, discriminating the color of a hand stimulus is a less cognitively demanding task than discriminating its laterality. In the former case, any attentional resources not already consumed could have 'spilled over' into the processing of the hand's grasp. In contrast, the more demanding laterality discrimination of Experiment 3 would have left fewer attentional resources available to process the remaining features of the action (Lavie, 1995, 2000).

The finding that the automatic imitation of grasp could be modulated by attending to a response-irrelevant dimension of the stimulus (i.e., its laterality) implies that different features of an action may be processed within separate modules in the action processing stream. The idea that actions are processed in a feature-based manner is consistent with current neuroimaging data, which show that cortical regions involved in action observation tend to encode different aspects of a perceived action. Premotor and parietal mirror areas, for example, are known to be sensitive to observed actions, and might subserve prehensile discrimination of the kind required in the 'Attend Grasp' tasks of this study. In contrast, areas such as the extrastriate body area (EBA) respond to images of human bodies or body parts, regardless of whether they depict an action (Chan, Peelen, & Downing, 2004; Downing, Jiang, Shuman, & Kanwisher, 2001; Urgesi, Candidi, Ionta, & Aglioti, 2007). In fact a recent TMS study has shown that the EBA is more sensitive to the perception of bodily form than the action that is depicted (Urgesi et al., 2007). It is therefore plausible that areas outside the mirror system, such as the EBA, could have been preferentially involved in decoding the laterality of the hand stimulus in Experiment 3, whereas parietal and premotor mirror areas encoded the action-related features of the stimulus, such as its grasp.

The modulation of automatic imitation by selective attention adds to the emerging view that observation–execution matching processes are susceptible to top-down influences. For example, Heyes et al. (2005) found that automatic imitation is not ubiquitous, but can be attenuated by training participants in a preliminary session to perform incongruent, rather than congruent, movements in response to an observed action (e.g., hand closing in response to hand opening). This suggests that experience and prior exposure to mismatched stimuli can also modulate the behavioral effect of automatic imitation.

In general, the fact that the covert simulation or overt expression of observed actions occurs only for actions that are attended should not be surprising. As social animals, we are confronted with a myriad of gestures in daily life, only a fraction of which are behaviorally relevant. Cognitive capacity limits prevent all of these actions from being processed simultaneously. We recently showed that the activity of action observation areas (specifically the left IFG, BA 45) during passive action observation can be suppressed by increasing the attentional load of a secondary task at fixation (Chong, Williams et al., 2008). These data indicate a key role for this area in gating the perceptual input to the mirror system and limiting the perceptual processing of those actions that are task-irrelevant.

Furthermore, if the visuomotor transformation of an action is as automatic as current data suggest (Fadiga et al., 1995; Stürmer et al., 2000; Wilson & Knoblich, 2005), some mechanism should exist to prevent actions from being imitated automatically (Kinsbourne, 2005). Data from patients with echopraxia and imitation behavior suggest the neural source of such inhibitory control. Patients with echopraxia compulsively imitate the actions of others, even when they are instructed to perform a separate task (Luria, 1966); patients with 'imitation behavior' imitate the gestures of an experimenter even when these gestures are socially unacceptable or odd (Lhermitte, Pillon, & Serdaru, 1986). Echopraxia has been associated with prefrontal and mesial cortical lesions, whereas imitation behavior is usually associated with fronto-orbital lesions. Both echopraxia and imitation behavior may therefore represent instances of a 'release' of prefrontal cortical inhibitory inputs to the mirror system that prevents overt movement production in normal individuals. This conclusion is supported by fMRI data in healthy participants, which show that having to perform an incongruent versus congruent finger movement activates prefrontal areas (including the frontopolar and middle frontal cortices), in addition to the precuneus and anterior parietal areas (Brass, Zysset, & von Cramon, 2001). Collectively, these data reveal the significance of the prefrontal cortex in inhibiting inappropriate imitation of perceived gestures. Such inhibition by the prefrontal cortex may underlie the behavioral suppression of automatic imitation found in the present study.

Finally, it is worth noting that, across all three experiments, congruency effects were manifest in mean initiation times alone, and not in mean transport times. Traditionally, chronometric studies of motor behavior consider initiation times to be a measure of the time required for response selection and preparation (Pratt & Abrams, 1994, but see also Meegan & Tipper, 1998). According to such accounts, the findings from Experiments 1 to 3 suggest that the interference between an observed and executed action manifests itself most clearly during the relatively early phases of action execution. However, once the movement is initiated, the present data imply that it is performed independent of any such competition. An obvious caveat to this claim is that transport times represent the net sum of several kinematic variables that may not be uniformly affected in a visuomotor priming study of the kind implemented here. Based on the present data, the absence of an effect in gross transport time suggests that any effects of automatic imitation on movement parameters, if present, may be relatively subtle. It remains for future investigations to more fully explore the kinematic consequences of executing an action during the observation of congruent versus incongruent hand postures.

In conclusion, our data show that the visuomotor transformation of an observed grasp can be modulated by directing attention towards features of the stimulus that are irrelevant to ongoing task requirements. These findings emphasize the role of selective processes in the filtering of task-irrelevant actions, and qualify previous claims that the process of observation–execution matching occurs automatically upon the perception of an action. More generally, our data are consistent with a growing body of empirical data which suggest that the processing of observed actions is susceptible to top-down modulation in numerous contexts, such as prior exposure. The selective filtering of task-irrelevant hands plays a critical role in naturalistic environments, by inhibiting the indiscriminate simulation and imitation of the many gestures we perceive in daily life.

Acknowledgements

The authors wish to thank Max Rademacher for technical assistance. The authors were supported by the National Health and Medical Research Council (NH&MRC) of Australia.

References

Bach, P., Peatfield, N. A., & Tipper, S. P. (2007). Focusing on body sites: The role of spatial attention in action perception. *Experimental Brain Research*, *178*, 509–517.

Bargh, J. A. (1992). The ecology of automaticity: Towards establishing the conditions needed to produce automatic processing effect. *American Journal of Psychology*, *105*, 181–199.

Bertenthal, B. I., Longo, M. R., & Kosobud, A. (2006). Imitative response tendencies following observation of intransitive actions. *Journal of Experimental Psychology: Human Perception & Performance*, *32*(2), 210–225.

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*, 3–22.

Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: Comparing symbolic, spatial, and imitative cues. *Brain and Cognition*, *44*(2), 124–143.

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The inhibition of imitative response tendencies. *NeuroImage*, *14*, 1416–1423.

Buccino, G., Binkofski, F., Fink, G., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*(2), 400–404.

Cant, J. S., Westwood, D. A., Valyear, K. F., & Goodale, M. A. (2005). No evidence for visuomotor priming in a visually guided action task. *Neuropsychologia*, *43*, 216–226.

Carpenter, W. B. (1874). *Principles of mental physiology, with their applications to the training and discipline of the mind and the study of its morbid conditions*. New York: Appleton.

Chan, A. W., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. *Neuropsychologia*, *43*, 115–127.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology*, *76*, 893–910.

Chevreul, M. E. (1833). Lettre à M. Ampère sur une classe particulière de mouvements musculaires. *Revue de Deux Mondes*, *2*, 258–266.

Chong, T. T.-J., Cunnington, R., Williams, M. A., Kanwisher, N., & Mattingley, J. B. (2008). fMRI adaptation reveals mirror neurons in human inferior parietal cortex. *Current Biology*, *18*, 1576–1580.

Chong, T. T.-J., Williams, M. A., Cunnington, R., & Mattingley, J. B. (2008). Selective attention modulates inferior frontal gyrus activity during action observation. *NeuroImage*, *40*(1), 298–307.

Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*, *11*, 1839–1842.

Cohen, J. D., Dunbar, K., & McClelland, J. L. (1990). Automaticity, attention and the strength of processing: A parallel distributed processing account of the Stroop effect. *Psychological Review*, *97*, 332–361.

Coricelli, G. (2005). Two-levels of mental states attribution: From automaticity to voluntariness. *Neuropsychologia*, *43*(2), 294–300.

Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia*, *40*, 492–502.

Darwin, C. (1872/1965). *The expression of the emotions in man and animals*. Chicago: University of Chicago Press.

Dimberg, U. (1982). Facial reactions to facial expressions. *Psychophysiology*, *19*(6), 643–647.

Dinstein, I., Gardner, J. L., Jazayeri, M., & Heeger, D. J. (2008). Executed and observed movements have different distributed representations in human aIPS. *Journal of Neuroscience*, *28*(44), 11231–11239.

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, *293*, 2470–2473.

Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, *15*(2), 213–218.

Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*(6), 2608–2611.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Gallese, V., & Metzinger, T. (2003). Motor ontology: The representational reality of goals, actions and selves. *Philosophical Psychology*, *16*(3), 365–388.

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*, 1159–1178.

Grezes, J., Armony, J. L., Rowe, J., & Passingham, R. E. (2003). Activations related to "mirror" and "canonical" neurones in the human brain: An fMRI study. *NeuroImage*, *18*(4), 928–937.

Hari, R., Forss, N., Avikainen, S., Kerveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences United States of America*, *95*, 15061–15065.

Hasher, L., & Zacks, R. (1979). Automatic and effort full, processes in memory. *Journal of Experimental Psychology: General*, *108*, 356–388.

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Cognitive Brain Research*, *22*, 233–240.

Hu, Y., & Goodale, M. A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience*, *12*, 856–868.

Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., et al. (2001). Reafferent copies of imitated actions in the right superior temporal cortex. *Proceedings of the National Academy of Sciences United States of America*, *98*(24), 13995–13999.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.

James, W. (1890). *The principles of psychology*. New York: Holt.

Kilner, J. M., Paulignan, Y., & Blakemore, S.-J. (2003). An interference effect of observed biological movement on action. *Current Biology*, *13*, 522–525.

Kinsbourne, M. (2005). Overlapping brain states while viewing and doing. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science. Volume 1: Mechanisms of imitation and imitation in animals* (pp. 210–214). Cambridge, MA: Bradford.

Koski, L., Wohlschläger, A., Bekkering, H., Woods, R. P., & Dubeau, M. C. (2002). Modulation of motor and premotor activity during imitation of target-directed actions. *Cerebral Cortex*, *12*, 847–855.

Lavie, N. (1995). Perceptual load as a necessary condition for selective attention. *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 451–468.

Lavie, N. (2000). Selective attention and cognitive control: Dissociating attentional functions through different types of load. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII*. Cambridge, MA: MIT Press.

Lhermitte, F., Pillon, B., & Serdaru, M. D. (1986). Human autonomy and the frontal lobes: I. Imitation and utilization behavior. A neuropsychological study of 75 patients. *Annals of Neurology*, *19*, 326–334.

Lotze, R. H. (1852). *Medizinische Psychologie oder Physiologie der Seele [Medical psychology or mental physiology]*. Leipzig: Weidmann'sche Buchhandlung.

Luria, A. R. (1966). *Higher cortical functions in man*. New York: Basic Books.

Meegan, D. V., & Tipper, S. P. (1998). Reaching into cluttered visual environments. *Quarterly Journal of Experimental Psychology*, *51A*(2), 225–249.

Milner, A. D., Paulignan, Y., Dijkerman, H. C., Michel, F., & Jeannerod, M. (1999). A paradoxical improvement of misreaching in optic ataxia: New evidence for two separate neural systems for visual localization. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *266*, 2225–2229.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113.

Pashler, H. (1998). *The psychology of attention*. Cambridge, MA: MIT Press.

Posner, M. I. (1978). *Chronometric explorations of mind*. Hillsdale, NJ: Erlbaum.

Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). Hillsdale, NJ: Erlbaum.

Pratt, J., & Abrams, R. A. (1994). Action-centered inhibition: Effects of distractors on movement planning and execution. *Human Movement Science*, *13*, 245–254.

Press, C., Bird, G., Flach, R., & Heyes, C. (2005). Robotic movement elicits automatic imitation. *Cognitive Brain Research*, *25*, 632–640.

Press, C., Gillmeister, H., & Heyes, C. (2006). Bottom-up, not top-down, modulation of imitation by human and robotic models. *European Journal of Neuroscience*, *24*, 2415–2419.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, *27*(0), 169–192.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., et al. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, *111*(2), 246–252.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3*, 131–141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*(9), 661–670.

Smith, A. (1759/1976). The theory of moral sentiments. In D. Raphael & A. Macfie (Eds.), *The Glasgow Edition of the works and correspondences of Adam Smith*. Oxford: Clarendon Press.

Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual gestures and postures: A study of imitation. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(6), 1746–1759.

Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nature Neuroscience*, *10*(1), 30–31.

Vaughan, K. B., & Lanzetta, J. T. (1980). Vicarious instigation and conditioning of facial, expressive and autonomic responses to a model's expressive displays of pain. *Journal of Personality and Social Psychology*, *38*, 909–923.

Vogt, S., Taylor, P., & Hopkins, B. (2003). Visuomotor priming by pictures of hand postures: Perspective matters. *Neuropsychologia*, *41*, 941–951.

Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusion and the real-time control of action. *Spatial Vision*, *16*, 243–254.

Wilson, M., & Knoblich, G. (2005). The case for motor involvement in perceiving conspecifics. *Psychological Bulletin*, *131*(3), 460–473.