Psychology Press
Taylor & Francis Group

Observed reach trajectory influences executed reach kinematics in prehension

Robert M. Hardwick[1,2] and Martin G. Edwards[2,3]

[1]School of Psychology, College of Life and Environmental Sciences, University of Birmingham, Birmingham, UK
[2]Faculté de Psychologie et des Sciences de l'Education, Institut de recherches en sciences psychologiques, Université Catholique de Louvain, Louvain-la-Neuve, Belgium
[3]School of Sport and Exercise Sciences, College of Life and Environmental Sciences, University of Birmingham, Birmingham, UK

Previous studies have demonstrated that the observation of action can modulate motor performance. This literature has focused on manipulating the observed goal of the action, rather than examining whether action observation effects could be elicited by changing observed kinematics alone. In the study presented here, observed reach trajectory kinematics unrelated to the goal of the action were manipulated in order to examine whether observed movement kinematics alone could influence the action of the observer. Participants observed an experimenter grasp a target object using either a normal or an exaggeratedly high reaching action (as though reaching over an invisible obstacle). When participants observed the experimenter perform actions with a high reach trajectory, their own movements took on aspects of the observed action, showing greater wrist height throughout their reaching trajectory than under conditions in which they observed normal reaching actions. The data are discussed in relation to previous findings which suggest that kinematic aspects of observed movements can prime action through kinematic or intention based matching processes.

Keywords: Mirror neurons; Action observation; Reaching; Prehension.

While there is a large volume of research that suggests that the neural processes of perception and action are distinct (see Milner & Goodale, 1992, 1995), other evidence suggests a coupling between these separate processes. An example of such coupling is provided by the reciprocal priming relationship whereby the presentation of a visual or motor stimulus[1] can prime subsequent action (Craighero, Fadiga, Umilta, & Rizzolatti, 1996; Edwards, Humphreys, & Castiello, 2003), and the preparation of an action can also prime perception (Symes, Tucker, Ellis, Vainio, & Ottoboni, 2008).

Data from neuroscience explain the mechanism underlying these priming effects. Single-cell recording studies conducted with primates have

[1] From here on, "motor stimuli" are defined as moving or static images of the hand.

provided evidence of "mirror neurons" in the premotor and parietal cortices, the firing activity of which are modulated both when the animal performs an action and also when they observe another agent perform a similar action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Subsequent neuroimaging studies have provided evidence of a similar action representation or "mirror system" in the human brain, again revealing activity in the premotor and parietal cortices (see Buccino et al., 2001; Iacoboni et al., 1999; Rizzolatti, Fadiga, Matelli, et al., 1996) and receiving input from the superior temporal sulcus (Blakemore & Frith, 2005). It is proposed that action observation priming effects utilize this mirror system, with the observation of action activating the observer's own motor system, facilitating a subsequent reactivation of the same process when the participant plans to execute an action.

Several human behavioural studies have demonstrated observational priming effects. Such studies have used both simple intransitive movements (Gowen, Stanley, & Miall, 2008; Kilner, Hamilton, & Blakemore, 2007; Kilner, Paulignan, & Blakemore, 2003; Stanley, Gowen, & Miall, 2007) as well as more complex goal-orientated actions such as manual prehension (Castiello, 2003; Castiello, Lusher, Mari, Edwards, & Humphreys, 2002; Dijkerman & Smit, 2007; Edwards et al., 2003; Griffiths & Tipper, 2009). For example, Edwards et al. (2003) used motion tracking to record the actions of participants following the observation of either a congruent or an incongruent action. Each trial began with the participant observing a priming action, which consisted of the experimenter reaching to and grasping an object. After a brief period in which their vision was occluded, the participant was required to perform a grasping action to an object in the same location as that observed in the priming event. However, the target object they grasped would be either the same size as the object observed in the priming event (congruent

priming; using similar grasp kinematics) or of a different size (incongruent priming; using different grasp kinematics). The data showed that prime congruency affected motor planning; the observation of congruent priming actions led to earlier occurrences of peak reach velocity and peak grasp aperture than in the observation of incongruent priming actions. In a further condition in which participants observed either a congruent or an incongruent object alone (without action), only effects on time to peak grasp aperture were present. This suggests that while the observation of a congruent *target object* alone was sufficient to provide priming for grasp preparation, observation of a congruent *action* may lead to further movement facilitation (i.e., a significantly earlier time to peak velocity). These data demonstrate that action observation can attune the observer's motor system to the subsequent performance of a congruent action and that while observing a target object alone can have some priming effects on grasping performance, observing the target object accompanied by a grasping action may lead to additional priming effects.

The presence of distractor objects during the observation of a grasping action has also been demonstrated to influence subsequently executed grasping actions in which no distractor is present. Castiello (2003) conducted a study in which participants observed actions of either a human or a robot model performing a manual prehension task. Previous studies had shown that the presence of a distractor object can modulate participant performance, interfering with normal movement kinematics (for a review see Castiello, 1999). Castiello (2003) hypothesized that observing a human model perform an action in the presence of a distractor would lead to priming effects on subsequent performance, even if the distractor object was removed prior to participants performing their actions. Participants observed a priming event in which the model grasped a sphere, which was presented either alone or in the presence of a distractor object of an identical or smaller size relative to the target. After a brief period in which the participant's vision was occluded, they were then required to grasp the target sphere, always doing so in the

absence of any distractor objects. The data revealed that the participants' maximal grip aperture was affected by the observation of the actions of the model, being smaller when they had observed the model grasp the target object in the presence of a small distractor than in both the other conditions. This effect was absent when a robotic model was used to demonstrate the action (and also when human models imitated the movements of the robot), indicating that the effects were not due to the presence or absence of distractor objects, but rather due to observing the natural kinematics of a human model with the intent to grasp the target object in the presence of a distractor (see also Castiello et al., 2002).

While the studies of Edwards et al. (2003) and Castiello (2003) demonstrated effects of sequential action observation on motor planning, data using concurrent action observation have revealed effects on late execution kinematics. Dijkerman and Smit (2007) manipulated object size congruency in a concurrent action execution task. Participants grasped a cube of a fixed size while observing the experimenter perform grasping or pointing actions. The experimenter would either perform a pantomimed grasping action to empty space (in the baseline condition) or perform a normal grasping action towards a congruently sized cube (identical to the participant's cube), a smaller cube, or a larger cube. Observing the experimenter concurrently grasping a larger object led to interference in the participant's own movement, as their grip aperture increased significantly compared to when they observed the pantomimed grasping and congruent grasping conditions. This modulation of grip aperture was not present when the participant observed the experimenter perform pointing actions, suggesting that specific kinematic aspects of the observed action led to the interference effect.

While these studies focused on the grasp component of the prehensile action, a recent series of experiments by Griffiths and Tipper (2009) examined the effects of action observation on the reach component. The experiments involved 2 participants alternately grasping target objects, allowing the effects of observing another person's

reaching actions to be examined on the subsequent trial. In certain conditions, participants were required to reach over an obstacle placed between their hand and the target object. Experiments in which the participants sat opposite each other, alternately grasping the same target object, revealed that observing their counterpart reach over an obstacle did not prime the movement paths of the participants. However, effects were revealed in later experiments that decreased the distance between participants. These experiments revealed effects of action observation when the observed action occurred within the peripersonal action space of the observer; when a participant observed a reaching action performed over an obstacle, their subsequent reaching actions simulated the action they had observed, showing higher reach trajectories than in conditions in which they observed a reaching action performed in the absence of an obstacle.

It is important to note that the studies reviewed here primarily manipulated goal-directed aspects of observed actions and that changes in action kinematics were not directly manipulated as independent variables. Some ambiguity therefore exists as to whether these effects are a result of the observation of *goal directed actions* or due to the observation of the *movement kinematics* used to achieve the goal. For example, Griffiths and Tipper (2009) elicited effects by having participants observe the goal-directed action of avoiding an obstacle that was placed in the actor's reach path. The priming effect revealed could therefore result from either the observed goal (avoiding the obstacle to grasp the object) or the observed kinematics (a movement with a high reach trajectory). However, more recent data suggest that goal-directed actions are not essential to modulate the firing of primate mirror neurons (Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009), and, furthermore, intransitive actions have also been demonstrated to elicit action observation effects in human behavioural studies (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000; Gowen et al., 2008; Kilner et al., 2007; Kilner et al., 2003; Stanley et al., 2007)

and human neuroimaging studies (Buccino et al., 2001; Iacoboni et al., 1999).

The experiment presented here examined whether the observation of non goal-directed movement kinematics could modulate action execution. Our hypothesis was that priming effects would occur from the observation of movement kinematics, even if these kinematics achieved no obvious goal. That is, compared to the observation of normal reaching actions, observation of reaching actions that follow an exaggeratedly high movement trajectory should modulate the participant's performance, and their actions should take on aspects of the observed movement (i.e., an increased reach height trajectory).

Method

Participants

Eight participants (6 female) aged 23–33 years, took part in the study. All were right-handed with normal or corrected-to-normal vision, and were naïve to the purpose of the study. Procedures were approved by the School of Sport and Exercise Sciences, University of Birmingham Ethics Committee. All participants gave written informed consent prior to their involvement in the study.

Equipment

Figure 1 illustrates the experimental set-up. Participants sat at a table covered with a black cloth and observed actions performed live by a 23-year-old male experimenter. A circular (25-mm diameter) reference marker was placed 50 mm from the table edge in front of the participant. The centre of this reference marker was 300 mm from the centre of the target object, a hollow plastic cylinder (white in colour, height 54 mm, diameter 54 mm, weight 19 g). A similar arrangement was provided for the experimenter, with reference markers both directly opposite and perpendicular to the participant, equidistant from an identical target object. The distance between the participant's and experimenter's objects (i.e., the distance between
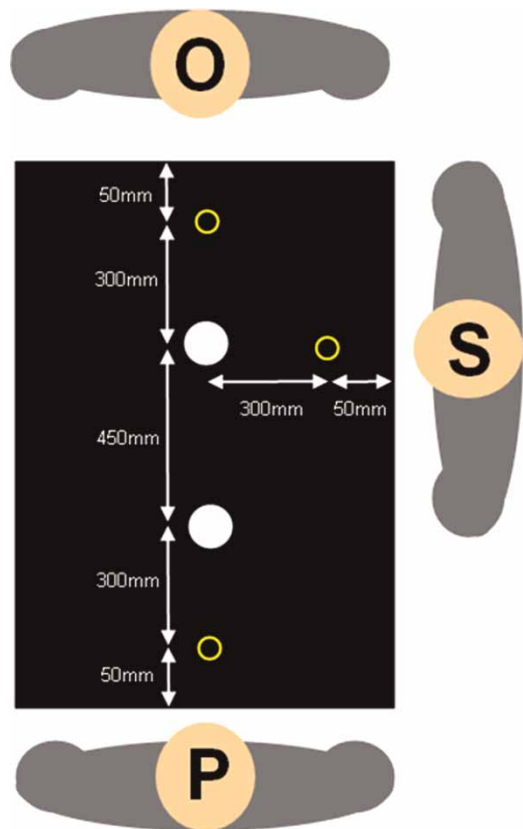

Figure 1. *Illustration of the experimental set-up. The participant (P) sat in a fixed position, while the experimenter sat in either an opposite (O) or a side-on (S) position. Small open circles represent the starting reference markers, while large filled circles represent the target object.*

targets of the observed and executed actions) was 450 mm.

All data were recorded using 14-mm diameter reflective markers placed on the wrists of the participant and experimenter and on top of each target object. Movements of these markers were recorded at 120 Hz using an eight-camera infrared Vicon system (Vicon MX) calibrated with millimetre accuracy.

Design and procedure

Throughout the experiment, participants were instructed to perform normal reaching and grasping actions to a target object. In each trial they
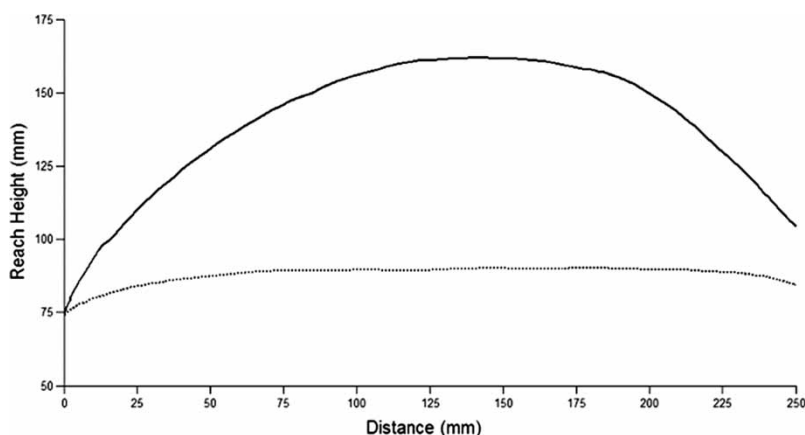
Figure 2. *Example reach trajectories for the movements of the experimenter. The dashed lower line presents a congruent (normal) reaching action, while the solid upper line shows an incongruent (high) reaching action. Note that while the distance between the starting reference maker and the target object was 300 mm, slight rotation of the hand during the reaching action led to the wrist marker covering a distance of only 250 mm.*

observed either a congruent (normal) reaching action, in which the experimenter reached directly to the target object in a natural manner, or an incongruent (high) reaching action, in which the experimenter reached towards the target object using an exaggeratedly high movement trajectory. Examples showing the differences in the trajectories of the experimenter's reaching actions are presented in Figure 2.

In order to examine the robustness of the priming effects, trials also varied in a 2 × 2 block design according to the timing between the observed and executed actions[2] and the position of the experimenter relative to the participant. In sequential timing blocks, participants first observed the movement of the experimenter, looking at their own target object and initiating their own action only when the experimenter's hand had returned to the starting reference marker. In concurrent timing blocks, the participant performed their actions in unison with the experimenter, attempting to initiate their movement and grasp their object at the same time as the experimenter (participants were instructed to observe the experimenter's action and to attend

to their own target object using their peripheral vision). Within each block, the experimenter was positioned either directly opposite or to the right side of the participant.

The experiment consisted of four trial blocks, the order of which was counterbalanced across participants. Each block consisted of 20 trials, and each participant completed 80 trials in total. The order of trials was randomized within each block.

Analysis

The dependent measure of participant reach height was recorded using a reflective marker placed on the wrist and was measured relative to the table surface. The analysis examined the independent variables of observed reach congruency (congruent "normal" reach or incongruent "high" reach), timing (sequential or concurrent), and experimenter position (opposite or side on). A further independent variable was also introduced to examine the height of the participant's reaching action at different temporal phases of their movement and was calculated by finding the height of the participant's wrist marker at the frames closest to the 25%, 50%, or 75% points of their

---

[2] Action observation priming of execution has been shown for sequential and concurrent timing relationships (e.g., Dijkerman & Smit, 2007; Edwards et al., 2003). Here we examined both timing modalities to test whether there were any resulting differences.

reach. Data were analysed using a $2 \times 2 \times 2 \times 3$ repeated measures analysis of variance (ANOVA).

Results

A number of trials were not included in the analyses; 30 trials were removed due to prolonged marker occlusion, and a further 14 trials were removed as outliers (i.e., values lying more than three standard deviations from the mean). Therefore, 93% of all trials collected were included in the analysis.

For the analysis of reach height, Mauchly's test indicated that the assumption of sphericity had been violated, and it was therefore corrected using Greenhouse–Geisser estimates of sphericity. The analysis revealed a significant main effect of reach congruency, $F(1, 7) = 9.22$, $p < .05$. This showed that participant reaching actions were relatively low when they observed congruent "normal" reaching actions and were comparatively higher when they observed incongruent "high" reaching actions (mean: congruent "normal" reach = 91 mm, incongruent "high" reach = 94 mm, SEM: 5.42 mm vs. 5.87 mm).

The results also revealed a significant main effect for the temporal phase of the reach trajectory, $F(2, 14) = 7.19$, $p < .05$. This revealed that participant reach height trajectory increased from the start of the movement to the midpoint and then reduced toward the end of the movement (mean: 25% phase = 95 mm, 50% phase = 99 mm, 75% phase = 84 mm, SEM: 7.19 mm vs. 5.99 mm vs. 4.82 mm). There was no significant main effect for timing, $F(1, 7) = 2.35$, $p = .17$, or position, $F(1, 7) = 3.55$, $p = .10$, and no significant interactions. Figure 3 presents the data for participant reach height trajectory.

Discussion

As hypothesized, the comparison between the observation of congruent "normal" reaching actions and incongruent "high" reaching actions revealed a modulation of participant movement performance. In comparison to the observation of congruent "normal" reaching actions, participants performed actions that were higher in trajectory (greater maximum wrist height) when they observed incongruent "high" reaching actions, even though they were instructed to perform normal reaching actions throughout the experiment. This was consistent with previous data examining the observation of congruent and incongruent actions (Castiello, 2003; Castiello et al., 2002; Dijkerman & Smit, 2007; Edwards et al., 2003; Griffiths & Tipper, 2009). As participants were instructed to perform normal reaching actions throughout the experiment, our data suggest that specific kinematic aspects of the observed movement were automatically imitated by the observer, even though these manipulations were not associated with an observed action goal.

While the study presented here demonstrates effects similar to those found by Griffiths and Tipper (2009), a disparity between these two datasets provides an interesting point for discussion. Griffiths and Tipper found effects on reach trajectory that were limited only to conditions in which the obstacle being avoided during the observed reaching action was presented within the peripersonal space of the observer. The participants did not have to avoid the obstacle themselves, nor did the obstacle have to be placed in the path they would later use when reaching to their target object, but they were affected by observed actions that avoided the obstacle when it was presented within their reaching space. In contrast, the actions performed by the experimenter in the study presented here occurred well outside of the extent of participant action space. When considered from a neurophysiological perspective, it is conceivable that this difference could be due to differential firing of mirror neurons. While early single-cell recording studies in the primate brain suggested that the distance from which an action was observed had no effect on the firing properties of mirror neurons (Gallese et al., 1996), a recent study has demonstrated differences in firing activity for actions observed from different relative distances. Caggiano, Fogassi, Rizzolatti, Thier, and Casile (2009) recorded the activity of 105 mirror neurons in area F5. Of these neurons, 28 demonstrated stronger firing activity when
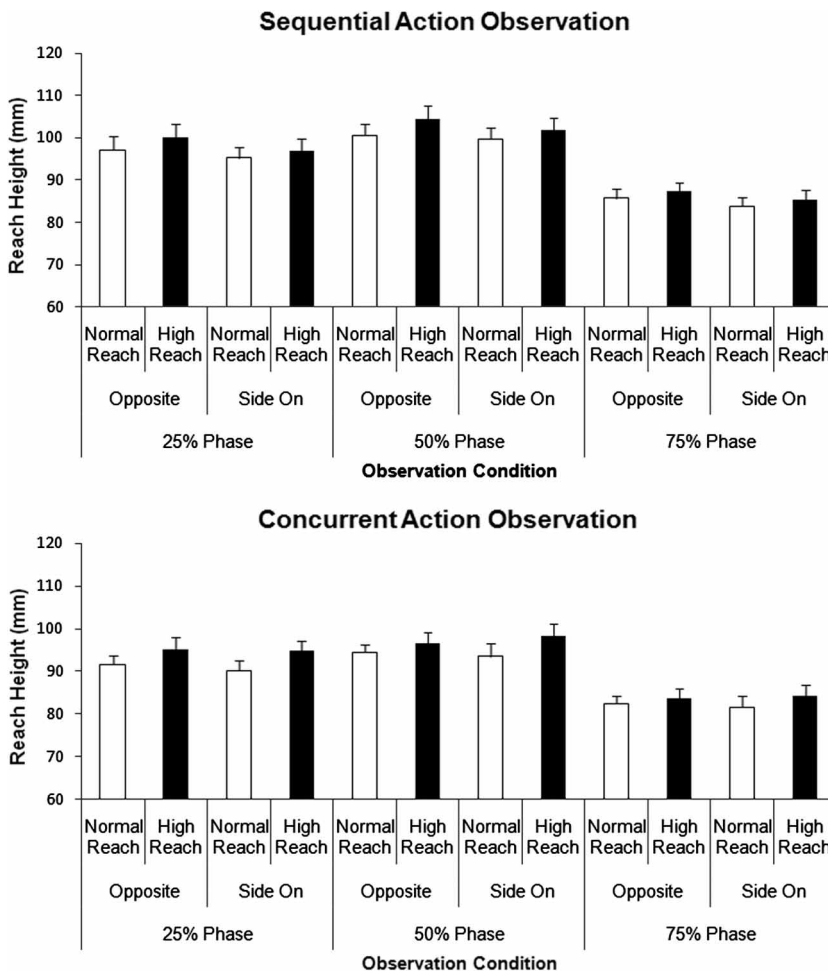
Figure 3. *Data for participant reach height. Upper panel shows data for sequential action observation, while lower panel shows data for concurrent action observation. Error bars show the average within-participant standard error of the mean.*

actions were presented to the monkey in peripersonal space, and 27 showed a preference for encoding actions presented in extrapersonal space, with the remaining 50 demonstrating no differences in their firing rate for the presentation of actions at different distances. Although the number of neurons examined that demonstrated preferences for peripersonal and extrapersonal space was comparable, this does not rule out the possibility that when considered across the whole brain, a majority of mirror neurons may show preferable firing activity for the observation of actions

in peripersonal or extrapersonal space, and future research may enlighten this issue.

An alternative explanation for the differences occurring between the study presented here and the study of Griffiths and Tipper (2009) would be the differences in the rationality of the observed actions across the two experiments. While Griffiths and Tipper presented participants with an explicit reason to employ a higher reach trajectory (to achieve the goal of avoiding an obstacle), the study presented here offered no such explicit reason for the experimenter to perform actions

with a high reach trajectory (i.e., there was no explicit goal associated with performing a higher reaching action). Several behavioural and brain imaging studies demonstrate a distinction between rational and irrational movements (Brass, Schmitt, Spengler, & Gergely, 2007; Gergely, Bekkering, & Kiraly, 2002; Gergely, Nadasdy, Csibra, & Biro, 1995). Work with preverbal infants has shown an ability to evaluate the rationality of an agent's goal-directed action (Gergely et al., 1995) and has also revealed a preference for imitation of irrational actions when it is explicitly clear that a more rational alternative has been avoided intentionally (Gergely et al., 2002). In the latter study, the authors propose that the spurning of a rational action may infer that the alternative method employed may be in some way advantageous in achieving the intended goal. Following this, Brass et al. (2007) demonstrated differential activation of the superior temporal sulcus when adult participants observed the same action in different contexts affecting its plausibility (such as using the knee to push a button when the hands were occupied compared to observing the same action when the hands were free). These differences in processing may explain why the effects in the study presented here remained present even outside of peripersonal space, especially as the human superior temporal sulcus is frequently associated with the human mirror system (see Blakemore & Frith 2005; Miall, 2003).

Modulation of the discharge of mirror neurons in primates has traditionally been demonstrated to occur in response to specific goal-directed actions, rather than to intransitive movements (Gallese et al., 1996, Rizzolatti, Fadiga, Gallese, et al., 1996). However, recent single-cell recording studies suggest that intransitive actions can also modulate the firing patterns of mirror neurons (Kraskov et al., 2009). Action observation studies with human participants have demonstrated that the observation of simple movement kinematics with no explicit goal can modulate brain activity (Buccino et al., 2001; Iacoboni et al., 1999) and behavioural performance (a phenomenon known as motor contagion; see Gowen et al., 2008; Kilner et al., 2007; Kilner et al., 2003; Stanley et al.,

2007). This led Blakemore and Frith (2005) to propose a mirror system for action observation composed of at least three levels: a low level where mirroring effects from observing simple biological movements occur (the level at which motor contagion effects would arise); a higher level at which specific goal-directed actions are mirrored (the level involving the eponymous mirror neurons); and a further theoretical level at which the intentions of others are mirrored. Therefore, some of the differences between our findings and those of Griffiths and Tipper (2009) could arise from different aspects of the mirror system being activated. In the study presented here, it is not readily apparent whether the action observation effects occured due to a modulatory effect driven by the participants attempting to imitate the *motor intention* of the experimenter (in a similar manner to the effects described by Castiello, 2003, and in accordance with Gergely et al., 2002; Gergely et al., 1995) or whether the effects were driven by the participants imitating the *motor kinematics* of the experimenter. However, both these possible explanations propose that the effects observed occurred on a different level to those of Griffiths and Tipper, as their goal-directed approach of having the observed model avoid an obstacle would theoretically activate the goal-directed aspect of this system. Activation of different aspects of the human mirror system could therefore explain the differences between the peripersonal space dependent effects seen in the study of Griffiths and Tipper and the effects presented here. Regardless of the level at which the modulation occurs, the automatic imitation effects from observing the experimenter's reaching actions revealed during the experiment presented here are consistent with previous literature (Castiello, 2003; Castiello et al., 2002; Dijkerman & Smit, 2007; Edwards et al., 2003; Griffiths & Tipper, 2009).

While our study may present movement-based, kinematically driven effects rather than goal-directed effects, the data do not necessarily challenge the goal-directed theory of imitation suggested by Bekkering, Wohlschlager, and Gattis (2000). The goal-directed theory suggests that observed actions are broken down then

recomposed by the observer, who will attend to key goals (such as the target object) but neglect aspects of lesser importance (such as the specific movement kinematics used to achieve those goals) when demands are placed on cognitive resources. In the study presented here, the goal (grasping the same target object) remained constant, allowing for more cognitive resources to be directed to the observed movement kinematics. To truly test this hypothesis, future studies could use the findings presented here while manipulating cognitive load to further examine effects on action priming.

The data presented illustrate an important point to consider in relation to the action observation literature previously discussed, highlighting the issue that effects of action observation are generally small in magnitude. A large difference between the experimenter's reaching trajectories (recording of experimenter kinematics throughout the study revealed a difference in experimenter wrist height between congruent "normal" reaching actions and incongruent "high" reaching actions of approximately 70 mm) led to a small, but significant, modulation of participant reach height (a mean difference of approximately 3 mm). While these modulatory findings were small in size, they are similar to the magnitude of the differences seen in previous studies examining grasp priming (Castiello, 2003; Castiello et al., 2002; Dijkerman & Smit, 2007; Edwards et al., 2003), and therefore it could be proposed that this is due to the experimental task; manual prehension is perhaps one of the most robust and overlearned skills available to examine and therefore may be resistant to experimental manipulation. However, studies of motor contagion have shown similar modest effects when participants performed experimental tasks with which they were likely to be far less familiar (see Kilner et al., 2007; Kilner et al., 2003). Together these data suggest that the goal-directed model proposed by Bekkering et al. (2000) requires further testing using motion tracking, as this provides an approach more sensitive to the subtle and often minute changes demonstrated in the action observation literature.

In terms of the other independent variables examined, the action observation effects presented here occurred regardless of the different timing modalities employed. It had been assumed that viewing an entire action before moving would allow for modification of motor planning (Edwards et al., 2003), while observing an ongoing action would only allow for modification of kinematics during execution (Dijkerman & Smit, 2007). If this had been the case, it would have been expected that the data would show a significant difference for the timing modality employed during the early phase of the movement, as the motor planning effects would modulate sequential action execution from the outset of the participant's movement, while concurrent action execution would only modulate participant performance once visual feedback of the reaching action occurred (presumably during the later phases of the action). In the study presented here, the reach height effects persisted across all timing conditions regardless of the different movement phases examined, and there was no significant interaction between the factors of temporal phase and observed reach type. A post hoc analysis examining the timing of the initial phase (25% temporal phase) of the participants' reaching actions provides an explanation for this finding. The only reliable effect revealed by this analysis was a significant main effect of observed reach congruency, $F(1, 7) = 28.15$, $p < .001$, showing that participant movements were fractionally faster when they observed reaching actions performed with a congruent "normal" reaching action than with an incongruent "high" reaching action (means: congruent "normal" reach = 283 ms, incongruent "high" reach = 287 ms, SEM: 20.43 vs. 20.68). Importantly, as no significant effects of timing were apparent, $F(1, 7) = 0.05$, $p = .84$, the data revealed that the average time at which the 25% phase of the reach component occurred was 285 ms into the reaching movement. As a number of studies estimate that the delay in using visual feedback to modulate ongoing action execution is in the order of 100–300 ms (e.g., Desmurget & Grafton, 2000; Miall, Weir, & Stein, 1985; Saunders & Knill, 2003, 2005; Savelsbergh, Whiting, & Bootsma, 1991), it is therefore likely that participant performance

would have already been modulated by visual feedback at this temporal phase in the concurrent action observation conditions, especially as the movement of the participant lagged slightly behind the movement of the experimenter (participants began their movements only when they had observed the experimenter begin to move). Therefore, future studies examining potential differences between sequential and concurrent action observation may wish to use externally generated cues as a sign to the participant and experimenter to begin their movements.

The analysis conducted also revealed that the effects of action observation demonstrated during this study occurred regardless of the position of the experimenter relative to the participant. Previous studies comparing actions observed from an egocentric frame of reference to an allocentric viewpoint (similar to our "opposite" position) have shown preferences for a compatible egocentric viewpoint (Gianelli, Dalla Volta, Barbieri, & Gentilucci, 2008; Vogt, Taylor, & Hopkins, 2003). The authors suggest that the improved performance was due to the greater congruency between the observed egocentric viewpoint and the observer's own natural viewpoint. As the study presented here effectively compared the observation of two incongruent positions (or perhaps more accurately an incongruent and neutral position when considering the relative spatial direction of the observed movements), the data presented are consistent with this proposal. Griffiths and Tipper (2009) conducted a series of experiments across which the position of the experimenter differed, but reported no differences dependent on the experimenter's location—only the position of the target obstacle the experimenter was required to avoid had any effect on the participant. While differences in brain activity when observing grasping actions from an egocentric or allocentric viewpoint have recently been demonstrated (Shmuelof & Zohary, 2008), it remains to be seen whether there is such a distinction between the observation of actions observed from different allocentric positions. These data may suggest that observed stimuli are interpreted in terms of whether they are egocentrically framed

or allocentrically framed, but that there are no distinctions for different viewpoints within these overall perceptual frameworks.

In conclusion, the study presented here replicates and extends the findings of Griffiths and Tipper (2009). While they used an implicit, goal-directed approach to manipulate the observed reach trajectory, the study presented here employed an explicit, movement-based approach. The explicit nature of the observed task in this study could be responsible for the effects extending to a range outside of the observer's peripersonal space, and different aspects of the mirror system may well be activated by these two similar yet distinct approaches to modulating observed reach trajectories. In summary, the observation of the experimenter's movement kinematics alone led to a small yet significant modulation of participants' reaching performance.

REFERENCES

Bekkering, H., Wohlschlager, A., & Gattis, M. (2000). Imitation of gestures in children is goal-directed. *Quarterly Journal of Experimental Psychology*, *53*, 153–164.

Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, *43*, 260–267.

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

Brass, M., Schmitt, R., Spengler, S., & Gergely, G. (2007). Investigating action understanding: Inferential processes versus action simulation. *Current Biology*, *17*(24), 1783–1789.

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*, 400–404.

Caggiano, V., Fogassi, L., Rizzolatti, G., Thier, P., & Casile, A. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science*, *17*, 403–406.

Castiello, U. (1999). Mechanisms of selection for the control of hand action. *Trends in Cognitive Science*, *7*, 264–271.

Castiello, U. (2003). Understanding other people's actions: Intention and attention. *Journal of Experimental Psychology*, *29*, 416–430.

Castiello, U., Lusher, D., Mari, M., Edwards, M., & Humphreys, G. (2002). Observing a human or robotic hand grasping an object: Differential motor priming effects. In W. Prinz & B. Hommel (Eds.), *Attention and Performance XIX* (pp. 314–334). Cambridge, MA: MIT Press.

Craighero, L., Fadiga, L., Umilta, C., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *Neuroreport*, *8*, 347–349.

Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*, 423–431.

Dijkerman, H. C., & Smit, M. C. (2007). Interference of grasping observation during prehension, a behavioural study. *Experimental Brain Research*, *176*, 387–396.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

Edwards, M. G., Humphreys, G. W., & Castiello, U. (2003). Motor facilitation following action observation: A behavioural study in prehensile action. *Brain and Cognition*, *53*, 495–502.

Fogassi, L., Ferrari, P., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*, 662–667.

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

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. In W. Prinz & B. Hommel (Eds.), *Attention and Performance XIX: Common mechanisms in perception and action* (pp. 335–355). Cambridge, MA: MIT Press.

Gergely, G., Bekkering, H., & Kiraly, I. (2002). Rational imitation in preverbal infants. *Nature*, *415*, 755.

Gergely, G., Nadasdy, Z., Csibra, G., & Biro, S. (1995). Taking the intentional stance at 12 months of age. *Cognition*, *56*, 165–193.

Gianelli, C., Dalla Volta, R., Barbieri, F., & Gentilucci, M. (2008). Automatic grasp imitation following action observation affects estimation of intrinsic object properties. *Brain Research*, *1218*, 166–180.

Gowen, E., Stanley, J., & Miall, R. C. (2008). Movement interference in autism spectrum disorder. *Neuropsychologia*, *46*, 1060–1068.

Griffiths, D., & Tipper, S. P. (2009). Priming of reach trajectory when observing actions: Hand-centered effects. *Quarterly Journal of Experimental Psychology*, *62*, 2450–2470.

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

Kilner, J., Hamilton, A., & Blakemore, S. J. (2007). Interference effect of observed human movement on action is due to velocity profile of biological motion. *Social Neuroscience*, *3*, 158–166.

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

Kraskov, A., Dancause, N., Quallo, M. M., Shepherd, S., & Lemon, R. N. (2009). Corticospinal neurons in macaque ventral premotor cortex with mirror properties: A potential mechanism for action suppression? *Neuron*, *24*, 922–930.

Miall, R. C. (2003). Connecting mirror neurons and forward models. *Neuroreport*, *14*, 2135–2137.

Miall, R. C., Weir, D. J., & Stein, J. F. (1985). Visuomotor tracking with delayed visual feedback. *Neuroscience*, *16*, 511–520.

Milner, D., & Goodale, M. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.

Milner, D., & Goodale, M. (1995). *The visual brain in action*. Oxford, UK: Oxford University Press.

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

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, 246–252.

Saunders, J. A., & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research*, 152, 341–352.

Saunders, J. A., & Knill, D. C. (2005). Humans use continuous visual feedback from the hand to control both the direction and distance of pointing movements. *Experimental Brain Research*, 162, 458–473.

Savelsbergh, G. J., Whiting, H. T., & Bootsma, R. J. (1991). Grasping tau. *Journal of Experimental Psychology, Human Perception and Performance*, 17, 315–322.

Shmuelof, L., & Zohary, E. (2008). Mirror-image representation of action in the anterior parietal cortex. *Nature Neuroscience*, 11, 1267–1269.

Stanley, J., Gowen, E., & Miall, R. C. (2007). Interference in performed movement during observation of a moving dot stimulus. *Journal of Experimental Psychology: Human Perception and Performance*, 33, 915–926.

Symes, E., Tucker, M., Ellis, R., Vainio, L., & Ottoboni, G. (2008). Grasp preparation improves change detection for congruent objects. *Journal of Experimental Psychology*, 34, 854–871.

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