Effects of Agency on Movement Interference During Observation of a Moving Dot Stimulus

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Human movement performance is subject to interference if the performer simultaneously observes an incongruent action. It has been proposed that this phenomenon is due to motor contagion during simultaneous movement performance–observation, with coactivation of shared action performance and action observation circuitry in the premotor cortex. The present experiments compared the interference effect during observation of a moving person with observation of moving dot stimuli: The dot display followed either a biologically plausible or implausible velocity profile. Interference effects due to dot observation were present for both biological and nonbiological velocity profiles when the participants were informed that they were observing prerecorded human movement and were absent when the dot motion was described as computer generated. These results suggest that the observer's belief regarding the origin of the dot motion (human–computer generated) modulates the processing of the dot movement stimuli on their later integration within the motor system, such that the belief regarding their biological origin is a more important determinant of interference effects than the stimulus kinematics.

Keywords: action observation, biological motion, mirror neurons

The processes underlying action imitation, by which visual information from action observation is converted into a program for motor execution, have been recently elucidated by findings showing that areas of the brain traditionally associated with motor production are also activated during action observation. These mirror neurons, located in the monkey ventral premotor cortex, are involved in both observation and execution of action (Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neuroimaging of human participants suggests that functionally similar brain areas exist in homologous areas of premotor cortex, providing common coding of motor execution and observation (e.g., Babiloni et al., 2002; Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Iacoboni et al., 1999).

Given the dual role of these mirror neuron sites, an interesting situation arises when an individual is required to perform a discrete action while simultaneously observing an incompatible action (e.g., incompatible in terms of the effector used or direction of movement). Under such circumstances, response initiation is delayed when there is a simple mismatch between the effector required for an action and the effector seen in the observed movement (e.g., lifting the index finger while observing lifting of the second finger; Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschlager, & Prinz, 2000). Similarly, visual presentation of a display showing an object or effector in an incompatible orientation relative to the required response (e.g., grasping a bar rotated either 0° or ± 60° from the displayed orientation) also delays response initiation relative to compatible observation–response trials (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Vogt, Taylor, & Hopkins, 2003).

These are all examples of how discrete responding is influenced by visual compatibility, with several possible explanations for the differences in reaction time—the visual stimuli might prime motor system processes, or the preparation of a motor response might influence the cognitive–visual processing of the stimuli (Craighero et al., 1999, 2002). More complex interactions between motor performance and observation systems can be tested by looking at compatibility effects during continuous movement execution and observation paradigms. Kilner, Paulignan, and Blakemore (2003) asked participants to move their arm in time with an experimenter, who was moving his or her arm in time with a metronome. Compared with congruent trials (in which the participant moved the arm in the same plane as the experimenter's moving arm), performing incongruent movement (participant moved his or her arm in a plane perpendicular to experimenter's arm movement) produced significantly greater variance in fingertip position (i.e., greater vertical position variance during horizontal movement and greater horizontal position variance during vertical movement).

This interference effect is hypothesized to be the result of motor contagion (Blakemore & Frith, 2005). It is presumed that during action observation, the processes underlying the imitation or understanding of action will lead to activation of premotor areas corresponding to the observed action (as outlined by Iacoboni, 2005), irrespective of their compatibility with an ongoing performed action. In the case of an observed incompatible action, it is

proposed that the motor program associated with the observed movement is then assimilated into the ongoing motor output, leading to motor production that is a partial blend of the two movements (Blakemore & Frith, 2005). This chain of events is supposed to begin in the superior temporal sulcus (STS; Iacoboni, 2005; Kilner et al., 2003), an area of the brain that has been strongly implicated in the perception of movement performed by another biological agent (e.g., Bonda, Petrides, Ostry, & Evans, 1996; Grezes, Costes, & Decety, 1999; Grezes & Decety, 2001; Grossman et al., 2000). This visual representation of the observed action is then hypothesized to indirectly feed into the ventral premotor cortex (Iacoboni, 2005).

Agency Influences the Interference Effect

A second major aspect of the Kilner et al. (2003) study was the comparison of effects from this interpersonal movement task with trials in which the participant observed a robotic arm making congruent–incongruent movements. The interference effect found for interpersonal movement trials was not apparent when the participant observed the robotic arm. This was taken as evidence for the limitation of mirror neuron processing to observation of a biological agent–effector, possibly because mirror neurons are only responsive to the observation of another biological agent (an effect of agency) or perhaps more specifically because the effect requires the observation of fine details of the arm movement (e.g., changes in limb posture). The authors also noted that kinematic differences between the two observed movements may have mediated some of the effect differences, as the robotic arm's velocity profile was distinctly flatter than that of the experimenter's arm movement.

Previous work has shown behavioral differences (e.g., in task reaction time) for tasks in which participants believe they are interacting with a human compared with interacting with a computer (Gowen & Miall, 2005; Ramnani & Miall, 2004). These behavioral differences have been attributed to the differential treatment of interactions with human and artificial agents—what is called the *intentional stance of the participant*. Taking an intentional stance requires one to view an entity as possessing intention, beliefs, and desires in order to predict its actions (Dennett, 1987).

However, some studies have shown interference effects caused by observation of nonbiological effectors. Press, Bird, Flach, and Heyes (2005) showed compatibility effects for response initiation during observation of both a human hand and of a two-pronged robotic manipulandum. This finding suggests that gross similarities between the required response and the observed action will allow compatibility effects. Similarly, a preliminary report from testing of the Kilner et al. (2003) interference paradigm with a more anthropoid robot (with a head, a torso, two arms, and two legs) has shown similar interference effects for observation of both humans and robots; joint configurations and movement velocity profiles for this robot were modeled on actual human movement (Oztop, Franklin, & Chaminade, 2004).

The aim of the present research was to clarify whether interference effects in a movement performance–observation paradigm can occur for nonbiological agents–effectors and whether this effect might be due to the motion profile of the viewed stimuli or to the purported agency of the movement. We contrasted the interference effect during the basic Kilner et al. (2003) paradigm (performing congruent and incongruent movements in time with a human experimenter) with a second set of trials in which the participant moves in time with a moving dot of light projected onto a screen. The velocity profiles used in the dot motion trials were manipulated to test whether the null interference effect for the robot arm conditions in the original report (Kilner et al., 2003) was due to the inconsistencies in velocity profile between the robotic arm and the human movement. Participants therefore viewed two sets of dot motion profiles. Biological dot motion was of a prerecorded arm movement that had been performed by the experimenter (in time with a metronome), whereas the nonbiological dot motion had a flat velocity profile and moved in a straight line without deviations in the perpendicular plane. Across two experiments, we manipulated the supposed agency of these stimuli—in the first experiment, participants were shown the dot motion stimuli without any additional information regarding their origin, whereas in Experiment 2, participants were either informed that the dot motion presentations were recordings of actual human movement or were computer-generated trajectories.

If the velocity profile of the observed movement is the important factor for producing the interference effect, we would predict that interference effects would be limited to trials in which the dot motion had a biological trajectory, irrespective of the participant's belief about what the dot represented (human movement or a computer-generated trajectory). Alternatively, if this belief is more important for producing the interference effect, we would predict an interference effect on the dot motion trials only when participants thought they were observing prerecorded human movement. To control for possible intersubject differences in susceptibility to interference, in each experiment, we also replicated the interpersonal movement–observation trials of the original paradigm (Kilner et al., 2003).

Experiment 1

The first experiment was designed to replicate the basic interference phenomenon for observation of human movement (Kilner et al., 2003) and to further test whether this interference effect occurs during observation of a distinctly nonbiological visual stimulus (a dot), regardless of whether this represented actual movement by a biological agent.

Method

Participants

The participants were 5 male and 5 female research staff or postgraduate students at the University of Birmingham (Birmingham, United Kingdom). Mean age was 33.1 years (range = 27–49 years). All were right-handed. The experiments were approved by the local ethics committee and were conducted in accordance with the Declaration of Helsinki. Participants provided informed consent prior to taking part in the experiments.

Movement Recording and Signal Processing

Fingertip position was recorded using the Optotrak 3020 active marker system (Northern Digital Instruments, Inc., Waterloo, Ontario, Canada). An infrared sensor was attached to a plastic thimble on the participant's right index finger, and sensor position was

recorded at 250 Hz with 0.01-mm spatial resolution; only data from the horizontal x-plane and the vertical z-plane were used in the analysis. The plane of instructed movement (e.g., the x-plane during a horizontal movement and the z-plane during a vertical movement) is referred to hereafter as the *dominant* plane; the orthogonal plane is referred to as the *error* plane. The experimenter's fingertip position was also recorded for those trials in which the participant moved in time with the experimenter but is not reported here.

Following data acquisition, fingertip position data were filtered with a 20-Hz Butterworth filter (all analysis conducted in MAT-LAB, Mathworks Inc., Natick, MA) prior to movement scoring. Each trial's data were split into single movement segments (e.g., from extreme left to extreme right made up one segment, and returning from right to left made up another segment). End points for each segment were detected by finding the data points at which velocity in the dominant movement plane crossed zero.

To quantify interference, we calculated the standard deviation of fingertip position within the error plane for each movement segment. The mean of these deviation scores was then calculated across all movement segments to give a single average of error plane deviation for each trial and for each participant.

Stimuli

The visual stimulus was a 1-cm diameter white dot, presented on a black background projected onto a white screen 1.9 m from the participant. The center of the projector screen was at a height of 1.55 m; the projector refresh rate was 60 Hz. The metronome for self-pacing movements was a sequence of tones presented at 1 Hz over headphones.

The biological dot motion was prerecorded data of James Stanley moving his arm in time with the audio metronome. The presented trajectories therefore included variation in the plane orthogonal to the dominant movement direction (e.g., there were fluctuations in vertical position during the presented horizontal movements). Data were scaled so that 50 cm in the recorded data corresponded to 50 cm on the projection screen. Movement frequency and the amplitude of the individual movement segments varied over the course of the recording (also true for trials in which the participant observed the experimenter moving). A section of the horizontal velocity profile of this biological dot motion is presented in Figure 1 (top). Table 1 presents summary data (movement amplitude, average deviation in the error plane, mean velocity, movement peak velocity, mean acceleration, peak acceleration, and mean movement period) for the horizontal and vertical biological motion presentations (duration = 40 s) and corresponding data for the nonbiological dot motion profile.

The nonbiological dot motion had a fixed amplitude of 50 cm on the projection screen and a fixed frequency of 0.5 Hz. Velocity was constant during each movement segment at 50 cm/s, with the dot instantly changing direction when reaching the end of each movement segment, as shown in the bottom of Figure 1 (note that the nonbiological motion velocity profile was identical for horizontal and vertical movements). For this stimulus, position orthogonal to the main plane of movement direction was invariable. The difference in the motion between the two dot trajectories was clearly visible to the participants.
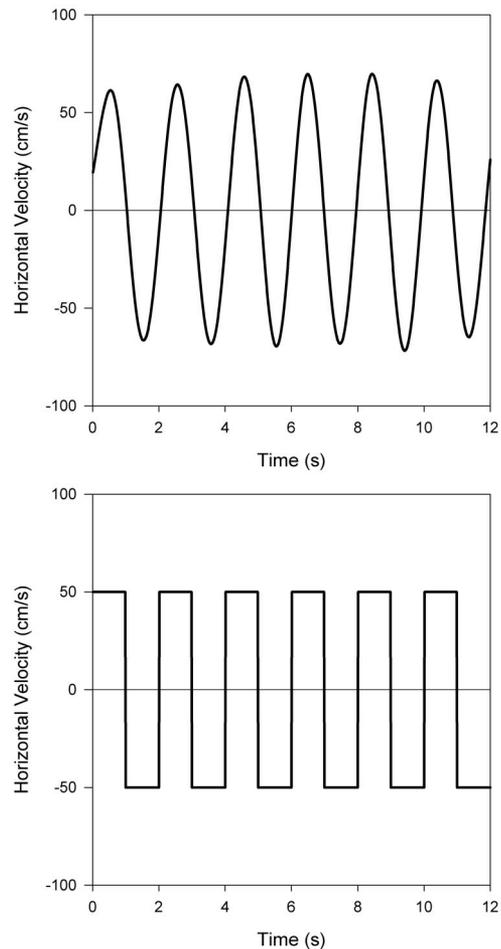

Figure 1. Horizontal movement velocity profile (cm/s) for biological dot motion (top) and nonbiological dot motion (bottom) visual stimuli.

Procedure

Testing interpersonal interference. Participants were instructed to perform 50-cm amplitude movements in all trials. Initially, each participant performed two practice trials (60-s duration) in time with the auditory metronome—one block of horizontal arm movements, followed by one block of vertical arm movements, while fixating a stationary circular target. Movements were timed so that the end points of each movement coincided with the tone. Following these practice trials, the participant was instructed to move his or her arm in phase with a gender-matched experimenter, who stood 190 cm away (toe-to-toe distance) and performed arm movements in time with the auditory metronome with eyes closed.

At the start of each trial, the participant was informed of the plane in which to move his or her arm as well as the plane the experimenter's arm would be moving in. Recordings began 2–3 s after both experimenter and participant were moving in phase and lasted for 60 s. Only the first 30 s of data were used for the analyses; initial analysis showed identical patterns of results for the first 30 s of data as for the entire 60-s trial.

Table 1
Means and Standard Deviations of Movement Parameters for the Biological (Horizontal and Vertical Motion) and Nonbiological (Identical for Horizontal–Vertical) Dot Motion Profiles Presented to Participants

	Amplitude (cm)		Error plane deviation (cm)		Mean velocity (cm/s)		Peak velocity (cm/s)		Peak acceleration (cm/s^2)		Period (s)	
Condition	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
Biological: Horizontal	43.5	2.9	0.54	0.22	43.4	3.1	83.7	6.4	19.8	1.8	0.98	0.04
Biological: Vertical	44.3	2.3	0.4	0.16	44.3	2.9	82.6	6.3	19.3	2.0	0.98	0.05
Nonbiological: Horizontal and vertical	50.0	0.0	0.0	0.0	50.0	0.0	50.0	0.0	100.0	0.0	1.0	0.0

Testing dot motion. Participants returned between 1 and 2 weeks after this initial test to perform the second part of the experiment, which consisted of two practice trials (as before), followed by eight trials moving in time with the dot stimulus. The dot motion trials were blocked by motion profile (biological or nonbiological), with the order of presentation counterbalanced across participants. Participants were not informed about how the dot stimuli were created but simply were asked to move in phase with the dot movement. Data recording for each trial lasted 30 s.

Data Analysis

Data for fingertip position standard deviation in the error plane were analyzed separately for the interpersonal movement task and the dot motion task. For the interpersonal task, a 2 (direction of participant's performed movement [horizontal or vertical plane]) × 2 (congruency of observed movement [congruent or incongruent]) analysis of variance (ANOVA) was used; for the dot motion task, a 2 (dot motion profile [biological or nonbiological]) × 2 (direction of participant's performed movement) × 2 (congruency of observed action) ANOVA was used.

For significant two-way interactions, *t* tests were performed between the appropriate levels of the factors involved using a Bonferroni α correction for multiple tests. For significant three-way interactions (i.e., for ANOVAs including dot motion as a factor), separate 2 (performed movement direction) × 2 (congruency of observed action) ANOVAs were calculated for the biological and nonbiological dot motion trials. Significant two-way interactions within these new ANOVAs were dealt with by *t* tests, again applying a Bonferroni correction.

Results

Interpersonal Movement Task

For the analysis of error plane fingertip standard deviation, there were significant main effects of performed movement direction, $F(1, 9) = 6.46$, $p = .032$, and congruency, $F(1, 9) = 25.16$, $p = .001$. The interaction between these factors was also significant, $F(1, 9) = 12.65$, $p = .006$. As seen in Figure 2, standard deviation in the error plane was generally greater during incongruent than congruent movement, although this was only significant during horizontal performed movements, $t(9) = 4.67$, $p = .001$ (adjusted α of .025), and not during vertical performed movement, $t(9) = 1.65$, $p = .132$ (adjusted α of .025). These results are in general agreement with Kilner et al. (2003).

Dot Motion Task

For the dot motion task, there was a significant main effect for congruency, $F(1, 9) = 7.98$, $p = .02$. There was also a significant three-way interaction among dot motion profile, performed movement, and observed congruency, $F(1, 9) = 11.7$, $p = .008$. The main effect of dot motion approached significance, $F(1, 9) = 4.18$, $p = .071$, with a trend toward higher standard deviations of error plane position for the biological stimuli ($M = 8.44$, $SE = 0.45$) than for nonbiological stimuli ($M = 7.47$, $SE = 0.63$). All other main effects–interactions were not significant, $F(1, 9) < 0.32$, $p > .588$.

The three-way interaction (see Figure 3) was tested by running two separate ANOVAs on the biological and nonbiological dot motion conditions. For the biological dot motion (see Figure 3, top), there was a significant main effect of congruency, with greater error plane standard deviation for the incongruent condition ($M = 10.16$, $SE = 0.97$) compared with the congruent condition ($M = 6.71$, $SE = 0.62$), $F(1, 9) = 6.47$, $p = .031$. Neither the main effect of performed movement nor the Performed Movement × Congruency Interaction were significant, $F(1, 9) < 0.14$, $p > .723$, indicating that the congruency effects were independent of the performed movement direction.
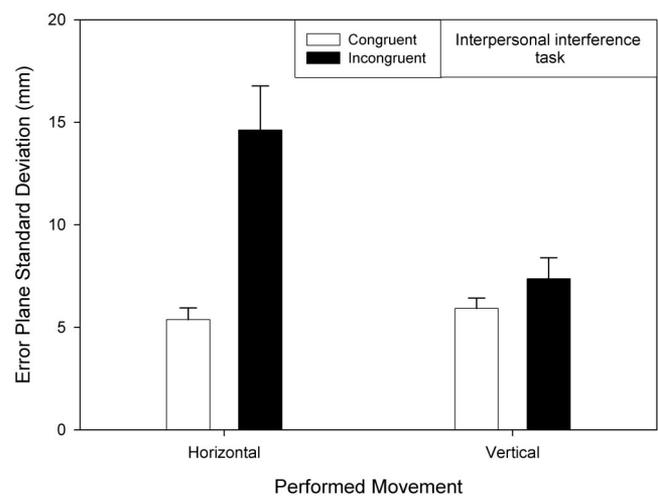

Figure 2. Experiment 1: Error plane standard deviation (mm) for horizontal and vertical performed movements during observation of an experimenter performing congruent and incongruent movement. Error bars represent plus one standard error of the mean.
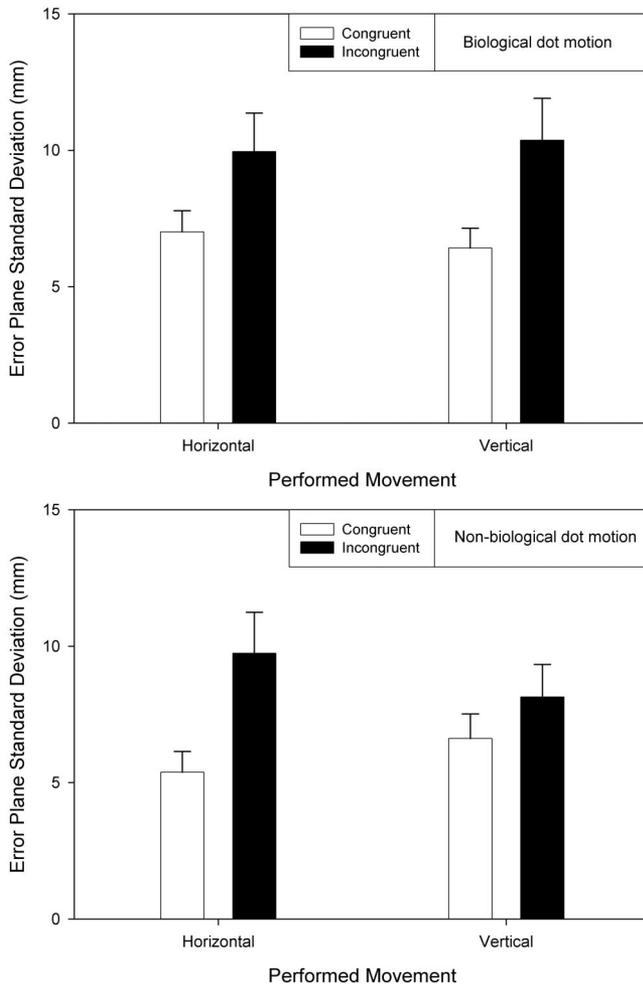
Figure 3. Experiment 1: Error plane standard deviation (mm) for horizontal and vertical performed movements during observation of a dot moving in a congruent or incongruent direction. Top: Biological dot motion profile. Bottom: Nonbiological dot motion profile. Error bars represent plus one standard error of the mean.

For the nonbiological dot motion (see Figure 3, bottom), the same pattern of results were found, with standard deviation in the error plane larger for incongruent trials ($M = 8.95$, $SE = 0.95$) than for congruent trials ($M = 6$, $SE = 0.67$), $F(1, 9) = 7.72$, $p = .021$. Again neither the main effect of performed movement nor the Performed Movement $\times$ Congruency Interaction were significant, $F(1, 9) < 1.03$, $p > .336$.

The three-way interaction showed a trend for the interference effect (incongruent trial standard deviation minus congruent trial standard deviation) to be stronger for biological than nonbiological dot motion for the vertical performed movement only, $t(9) = 2.87$, $p = .018$ (corrected $\alpha = .0125$ for four tests; other comparisons, $t[9] < 1.15$, $p > .281$).

Discussion

The results from the interpersonal movement task were a partial replication of Kilner et al. (2003). Interference in movement performance was found during incongruent movement observation but only for horizontal performed movements. The Kilner et al. article reported a nonsignificant interaction between performed movement direction and congruency, with a trend toward a smaller interference effect for vertical arm movements compared with horizontal arm movements (S. J. Blakemore, personal communication, June 2005). However, in the current experiment, the movement direction effect was not significant in the second session for testing the effect of dot motion trajectories, whereas the main interference effect remained highly significant.

Hence, the interference effect was apparent when participants moved in time with a dot stimulus without being given any explicit information about the authorship or agency of the dot. Although this interference effect appeared to be more robust for the biological dot motion, it was still significant for the nonbiological dot motion. Press et al. (2005) likewise reported that response compatibility effects were stronger for observation of a human hand than for observation of a robotic manipulandum.

This finding suggests that the interpersonal interference effect reported by Kilner et al. (2003) and reproduced here is unlikely to be limited to observation of another person but can be elicited by other moving stimuli as well. Interference also appears relatively insensitive to the kinematic qualities of the viewed motion, although it is possible that the motion profiles of the two stimulus sets were not sufficiently different from each other.

The fact that this sample showed interference effects to an abstract stimulus during both biological and nonbiological motion profiles raises the question of why no interference effect was previously found for movements performed in time with a robotic arm (Kilner et al., 2003). The current experiment was not controlled in some aspects that may have bearing on our findings. Participants were not truly naive in the second part of the experiment, having previously completed the interpersonal movement task (introducing potential order effects). It is likely that some participants inferred that one or both of the dot motion conditions were actual human movement. If this was the case, then the interference effect might be mediated by the perceived agency of the viewed movement (human vs. computer controlled). A second experiment was designed to resolve this confound by having participants complete the dot motion trials prior to performing the interpersonal movement task and also by explicitly manipulating the instructions they were given regarding the dot motion profiles.

Experiment 2

Experiment 2 was designed to control for participant experience in the interference task as well as explicitly manipulating the reported agency of the dot motion presentations. A new set of participants was tested with the dot motion task prior to performance of the interpersonal movement task, hence removing possible order effects. Half of the participants were explicitly informed that the dot motion stimuli were recordings of human movement, whereas the other half were informed that the dot motion stimuli followed computer-generated trajectories. The dot motion profiles used were identical to those in Experiment 1. This experiment also allowed us to check that the results of Experiment 1 were not simply due to viewing moving stimuli but were due to a human-movement interpretation of the stimuli. We hypothesized that participants would show an interference effect on the dot

motion task when they believed that the dot motion stimuli were recorded human movements but not when they believed the motions were computer generated. On the basis of Experiment 1, we expected similar patterns of interference in the human-agent instruction condition for the biological and nonbiological stimuli.

Method

Participants

A new group of 20 right-handed participants (10 male, 10 female) were recruited through the School of Psychology experiment recruitment system at the University of Birmingham and were paid £5 ($9.81) for taking part. Mean age was 25.4 years (range = 20–48 years).

Procedure

The stimuli and stimulus presentations were identical to Experiment 1, except that all trials lasted 30 s. In a single session, participants completed the practice trials, followed by the dot motion trials, and then the interpersonal movement task. The two main changes from Experiment 1 were that participants were not initially informed that they would perform the task while moving in time with an experimenter, and the ordering of trials was different from the first experiment. Only the instructions for the dot motion task differed between the two groups.

In the human-agent group, participants were informed that the moving dots were recordings of human movement. Also, prior to each trial, the experimenter informed the participant, "On this trial, you will be watching a recording of a person moving their arm in the (horizontal–vertical) plane." For the computer-agent group, the participant was informed that he or she would observe and move in phase with "a computer-generated moving dot," and the experimenter introduced each trial by saying, "On this trial, the dot will be moving in the (horizontal–vertical) plane." No distinction was drawn between the two dot motion conditions, other than the participant being told that he or she would see two slightly different patterns of motion. Following completion of all of the dot movement trials, the participant then completed the interpersonal movement task with the gender-matched experimenter, with the same set of instructions for both groups (see Experiment 1).

Analysis

The analysis was similar to Experiment 1, with the addition of the between-subjects agency instructions variable (human or computer). For the dot motion task, this gave a 2 (instruction regarding the dot motion stimulus [human or computer agent] × 2 (dot motion profile [biological or nonbiological]) × 2 (direction of participant's performed movement [horizontal or vertical plane]) × 2 (congruency of observed action [congruent or incongruent]) mixed ANOVA.

The agency instruction grouping variable was also used for the analysis of the interpersonal movement task to control for possible differences on the basic task between these two groups. This gave a 2 (agency instruction group) × 2 (direction of participant's performed movement) × 2 (congruency of observed movement) mixed ANOVA for the interpersonal task.

Results

Dot Motion Task

The analysis indicated a significant main effect of congruency, $F(1, 18) = 7.3$, $p = .015$, as well as a significant interaction between congruency and agency instruction group, $F(1, 18) = 5.31$, $p = .03$. Analyzing the congruency main effect separately for the two groups indicated a significant congruency effect for the human-agent instruction group, $F(1, 18) = 10.03$, $p = .011$, but no significant main effect of congruency for the computer-agent instruction group, $F(1, 18) = 0.9$, $p = .769$. These data are presented in Figure 4. Neither the main effect of agency instruction group nor other interactions involving this factor were significant, Fs (1, 18) < 2.02, $ps > .172$.

Two other interactions were significant: a two-way interaction between performed movement direction and congruency, $F(1, 18) = 7.91$, $p = .012$, and a three-way interaction among dot motion stimulus, performed movement direction, and congruency, $F(1, 18) = 6.66$, $p = .019$. This three-way interaction is presented in Figure 5.

Breaking the three-way interaction into two separate ANOVAs for the biological and nonbiological dot stimuli (averaging over the instruction group factor) showed that for the nonbiological dot stimuli (see Figure 5, bottom), there was only a significant main effect of congruency, $F(1, 19) = 4.48$, $p = .048$. Error plane deviations were higher for the incongruent condition ($M = 9.02$, $SE = 0.68$) than the congruent condition ($M = 7.84$, $SE = 0.59$). However, for the biological dot motion stimuli, the interaction between performed movement direction and congruency was significant, $F(1, 19) = 15.41$, $p < .001$. As displayed in the top of Figure 5, the difference between the perform horizontal–incongruent and perform horizontal–congruent conditions was not significant, $t(19) = 1.53$, $p = .144$, whereas error plane deviations in the perform vertical–incongruent condition were significantly higher than error plane deviations in the perform vertical–congruent condition, $t(19) = 4.34$, $p < .001$. As these interactions
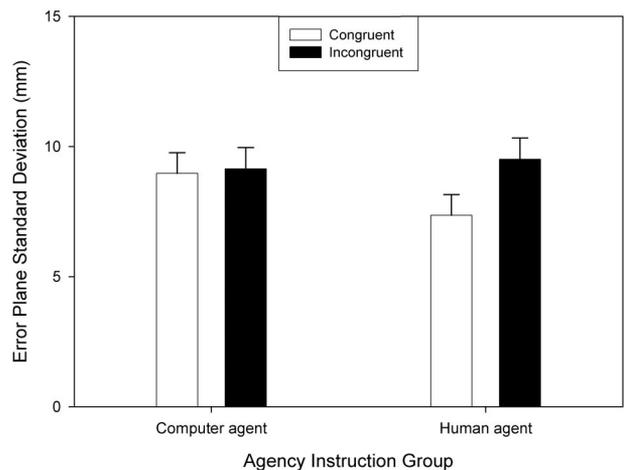
Figure 4. Experiment 2: Error plane standard deviation (mm) for the instructed computer-agent and instructed human-agent groups during observation of a dot moving in a congruent or incongruent direction. Error bars represent plus one standard error of the mean.

were calculated on average over both agency instruction groups and the omnibus ANOVA had indicated that the congruency effect was dependent on the agency instruction, these results are of limited interest.

However, these interactions can be more clearly explained by rearranging the analysis so that one is testing Dot Motion × Performed Movement × Observed Movement Direction (rather than congruency):[1] In this manner, the former three-way interaction now expresses a statistically identical interaction between dot motion profile and observed movement direction, and the former two-way interaction between performed movement and congruency becomes a significant main effect of observed movement direction. It should be noted that under this reanalysis, the previous Congruency × Agency Instruction Group interaction remains significant as a three-way interaction among observed direction, performed movement direction, and agency instruction group.

The interaction between dot motion stimulus and observed movement direction is displayed in Figure 6. Breaking down this
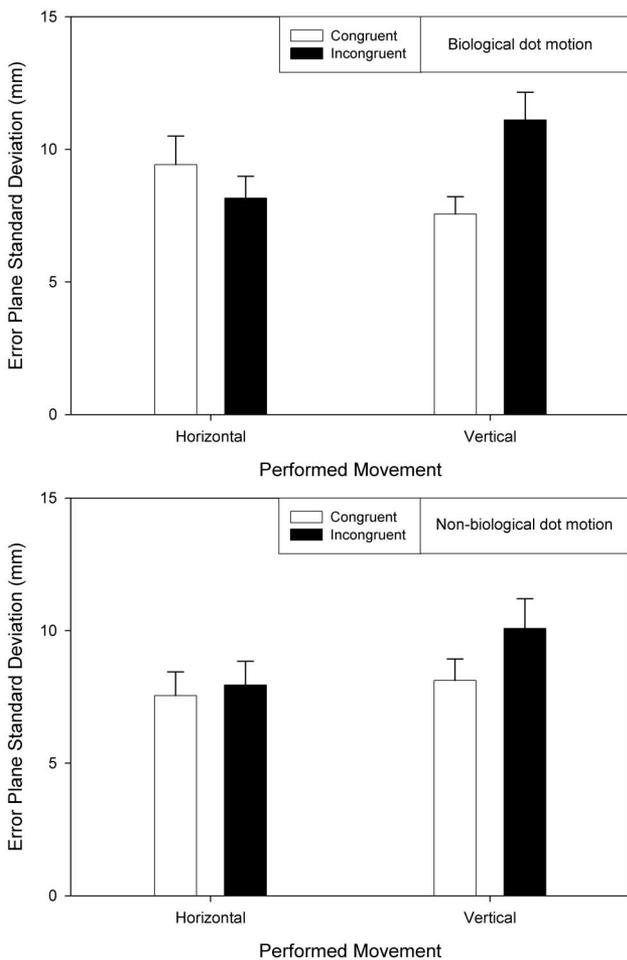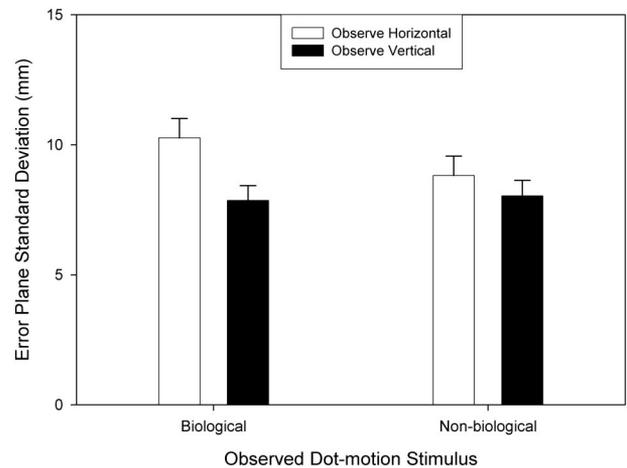

Figure 6. Experiment 2: Error plane standard deviation (mm) for the biological dot motion and nonbiological dot motion conditions during observation of a dot moving in the horizontal or vertical plane. Data are averaged across the instructed human- and computer-agent groups. Error bars represent plus one standard error of the mean.

interaction indicated that for the biological motion stimuli, observing a horizontal movement produced more error plane position deviation than observing a vertical movement, $t(19) = 3.93$, $p = .001$. For the nonbiological dot motion stimuli, there was no difference between observing horizontal or vertical movement, $t(19) = 1.12$, $p = .279$.

It is worth repeating that these effects of observed movement direction were independent of the agency instruction factor, as indicated by the nonsignificant higher level interaction between this three-way interaction and the agency instruction factor, $F(1, 18) = .094$, $p = .763$.

Interpersonal Movement Task

The analysis of the interpersonal task data indicated a significant main effect of congruency, $F(1, 18) = 23.59$, $p < .001$. There were larger deviations in the error plane for the incongruent condition ($M = 9.58$, $SE = 0.61$) than for the congruent condition ($M = 7.27$, $SE = 0.61$).

The main effect of performed movement direction approached significance, $F(1, 18) = 4.02$, $p = .06$. The trend was toward greater error plane deviations when performing vertical movements ($M = 9.28$, $SE = 0.79$) compared with when performing horizontal movements ($M = 7.27$, $SE = 0.57$). The three-way interaction among agency instruction group, performed movement, and congruency also approached significance, $F(1, 18) = 3.95$, $p = .062$. No other main effect or interaction was significant, $Fs(1, 18) < 1.61$, $ps > .221$.

The three-way interaction is displayed in Figure 7, with data for the human-agent instruction group shown in the top panel and data

Figure 5. Experiment 2: Error plane standard deviation (mm) for horizontal and vertical performed movements during observation of a dot moving in a congruent or incongruent direction. Top: Biological dot motion profile. Bottom: Nonbiological dot motion profile. Data are averaged across the instructed human- and computer-agent groups. Error bars represent plus one standard error of the mean.

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[1] The *observe horizontal* condition comprises the perform horizontal–congruent observation trial and the perform vertical–incongruent observation trial, and the *observe vertical* condition comprises the perform vertical–congruent observation trial and the perform horizontal–incongruent observation trial.
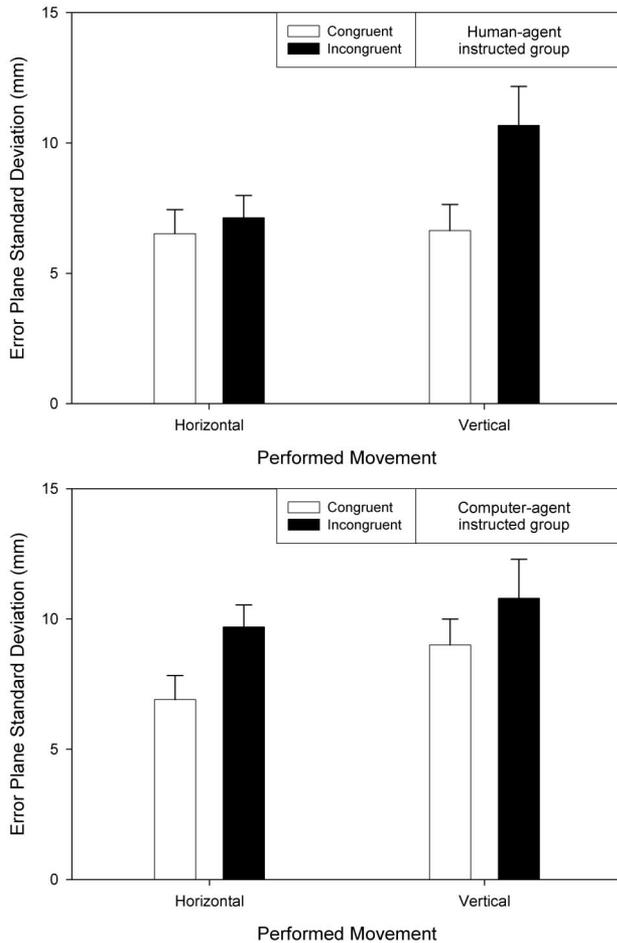
Figure 7. Experiment 2: Error plane standard deviation (mm) for horizontal and vertical performed movements during observation of an experimenter performing congruent and incongruent movement. Top: Human-agent instruction group. Bottom: Computer-agent instruction group. Error bars represent plus one standard error of the mean.

for the computer-agent group in the bottom panel. The interaction indicated a trend for the participants in the human-agent group toward a smaller congruency effect during performance of horizontal movement compared with during vertical movements.[2]

Discussion

The congruency effect previously observed for the dot motion task in Experiment 1 appears to be dependent on the participant believing that he or she is observing human movement: The congruency effect was not apparent for those participants who were told the dot motion stimuli were computer generated. As participants performed the dot motion task prior to the interpersonal movement task, we can rule out the possibility that prior task experience, or prior experience of the interference effect, is responsible for the interference effect during the dot motion task. Figure 4 suggests that the compatibility effect may be due to facilitation of movement performance in the congruent condition rather than interference in the incongruent condition (with the

latter interpretation drawn by Kilner et al., 2003), because the error plane standard deviation for incongruent stimuli in the human-agent instruction group was comparable with that found for both congruent–incongruent stimuli in the computer-agent instruction group. However, given the between-subjects nature of this comparison and the absence of an attentionally matched neutral task condition, further research is needed to determine whether this compatibility effect is actually caused by interference on incongruent trials, facilitation on congruent trials, or both.

Once again, interference effects were consistent across biological and nonbiological dot motion trajectories, supporting our hypothesis that the reported agency of the dot motion is more important than the actual velocity profile of the motion for producing this interference effect.

Of note, the results also indicate that the biological and nonbiological motions had different effects on performed movements: For the biologically derived stimuli, observing the horizontal dot motion introduced more deviation in the error plane fingertip position than did observing the vertical dot motion. This result can perhaps be explained in terms of the visual stimuli, in that the biological horizontal recording was more variable than the vertical recording[3] (with regard to motion in the error plane perpendicular to dot motion direction). As this effect operated independently of the agency instruction factor and did not qualify the significant Congruency $\times$ Agency Instruction interaction, we suggest that simply watching a variable movement produced increased variability in the participant's movement, without an effect of agency.[4]

It is important to note that the interpersonal interference effects were seen for both groups of participants in the subsequent test, which rules out the possibilities that the computer-agent group either performed the basic task differently from the participants in Experiment 1 or the human-agent group, or were somehow impervious to the interference phenomenon. Presentation of the dot motion stimuli did not produce the classic interference effect when participants had been told that the dot was computer generated, which suggests that the interference effect found in Experiment 1 was not simply due to viewing a moving stimulus.

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[2] Performing separate 2×2 ANOVAs on the two groups showed significant main effects of congruency for both, $Fs(1, 18) > 10.03$, $ps < .012$. The interaction between performed movement direction and congruency still only approached significance in the human-agent instruction group, $F(1, 18) = 3.84$, $p = .082$, and so this interaction was not followed any further.

[3] An unpaired t test, comparing the deviations for all of the movement segments presented as the biological horizontal and biological vertical dot motion stimuli (see Table 1), confirmed that the horizontal movement had more vertical position deviation than the vertical movement had horizontal plane deviations, $t(71) = 3.26$, $p = .002$.

[4] Applying the same analysis strategy to the data of Experiment 1 also indicated a significant interaction between dot motion stimulus and observed movement direction, equivalent to the three-way interaction reported in that section, $F(1, 9) = 11.7$, $p = .008$. Follow-up t tests revealed that error plane deviations were greater in the observe horizontal–biological motion condition (which had variability in the error plane) than in the observe horizontal–nonbiological motion condition (which was invariable in the error plane), $t(9) = 4.44$, $p = .002$. Other comparisons: $t(9) < 1.02$, $p > .337$. This result is consistent with our interpretation of Experiment 2.

General Discussion

The experiments reported here have replicated the findings of Kilner et al. (2003) regarding interference effects during interpersonal continuous movement execution–observation. Furthermore, this interference effect also was apparent when viewing a moving dot stimulus, but only if the participant had previously performed interpersonal movement trials (Experiment 1) or had been told that the dot motion represented human movement (the human-agent instruction group in Experiment 2). If participants were informed that the dot motion was computer generated (the computer-agent group in Experiment 2), movement performance was influenced by the amount of visual noise in the observed stimulus (which also had an effect on the human-movement group in Experiment 2, in addition to the congruency effect), rather than by compatibility between observed and performed movement directions.

Although the participants in Experiment 1 were not given any explicit information regarding the origin of the dot trajectories, it is possible that they had enough knowledge of the task to interpret these dot movements as the result of human movement. In Experiment 1, the interference effect showed a trend toward being less strong for the nonbiological dot motion (a significant interaction concerning the vertical performed movement), although subsequent reanalysis concentrating on the direction of the observed movement, rather than on the congruency between observed and performed movements, appears to explain this result more clearly. The biological horizontal motion dot stimulus appeared to induce extra error plane deviations into the participant's movement.

The results therefore suggest that the lack of interference found during interactions with a robot (Kilner et al., 2003) was not due to kinematic differences between the robotic and human arm movements. Instead, the results of our experiments suggest that the agency of the movement stimuli (human vs. artificial agent) mediates the interference effect. It is interesting to note that in a visuomotor action imitation task, Press et al. (2005, Experiment 1) found response compatibility effects for both human hands and robotic hands. A second set of experiments from the same group (Press, Gillmeister, & Heyes, 2006) found an enhanced compatibility effect when the robotic hand stimuli were visually similar to the human hand stimuli. These authors concluded that these compatibility effects are driven by bottom-up visual properties of the observed stimulus, rather than by top-down interpretation of the stimulus as human or robot. It is important to note that the stimuli used in these experiments were less ambiguous than those used in our own experiments, and even the two-pronged robotic manipulandum bears a gross similarity to a human hand. These similarities may drive the automatic imitation mechanisms described by Press et al. (2005, 2006). In the current experiment, the use of dot stimuli precludes any gross similarity in effector shape between the performed movement and the observed movement. Thus, the effect of the agency manipulation that we report may be dependent on ambiguity in the observed visual stimuli. The difference in movement interference effects caused by biological and nonbiological motion stimuli in Experiment 1 and the increased error plane deviations during observation of the horizontal biological motion stimuli in Experiment 2 (independent of the agency instruction and the congruency effect) suggest that some bottom-up effects of stimulus motion were present in the current experiments as well as the top-down effects of agency belief.

The Effect of Agency on Perceived Motion

It has been suggested that the interference effect takes place at the level of premotor mirror neurons but that the process starts with visual processing of movement in the STS (Blakemore & Frith, 2005; Kilner et al., 2003). The STS is known to be responsive to the observation of human movement (e.g., Grezes & Decety, 2001). However, in all of these previous paradigms, the agent was never in doubt. Of note, the STS is also responsive to viewing a series of multiple moving light points that represent biological movement (e.g., a person walking; Grezes et al., 2001; Grossman et al., 2000). That abstract stimuli can activate this area suggests that it is responsive to the motion of the viewed stimulus, rather than specifically to observation of moving biological agents. In our experiments, when participants were told that they were viewing a person's movement, observing the dot motion stimuli appeared to generate equivalent interference to that found when observing an actual moving person. Thus, the relevant processing of the dot motion might involve the participant imagining the (unobserved) arm movement that caused the observed dot motion, leading to activation of premotor neurons and hence the interference effect. The interference effect was present or absent depending on the participant's belief about the origin of the dot trajectory. Therefore, these findings imply that the system responsible for the processing of biological movement can be engaged by the interpretation of abstract dot stimuli as human movement. Alternatively, it is possible that the effects of the human-agency instruction were to simply increase attention toward the dot motion stimulus so that any bottom-up effects caused by the dot trajectories were enhanced under these instructions. Although this is possible, the results of Experiment 2 suggest that this may not be the case. The reported stimulus-driven effects for the biological-motion horizontal stimulus were apparent for both the human-agent and computer-agent instruction groups. Furthermore, this effect was independent of the congruency effect, which was only found in the human-agent instruction group. If attentional differences between the agency conditions produced bottom-up interference effects in this experiment, we would have expected the stimulus-driven effect of the biological motion stimulus to be absent in the computer-agency group.

The hypothesis that the effects are due to imagined human action is supported by evidence suggesting that simulation of observed movement can take place in the absence of action observation. First, premotor mirror neurons in the macaque remain active when the end point of an observed action is occluded from sight (Umiltà et al., 2001). Similarly, activity in the anterior part of macaque STS is noted if an observed walker momentarily disappears from view behind an occluding panel (Baker, Keysers, Jellema, Wicker, & Perrett, 2001). In human participants, imagined movement (Ruby & Decety, 2001) or implied motion (in static images; Kourtzi & Kanwisher, 2000; Senior et al., 2000) can also activate motion processing areas. As the neural site(s) that mediate the interference effect in the interpersonal movement task still remain untested, the process by which the participant's beliefs about the observed dot motion may alter these processes also remains speculative. It is possible that STS processing of dot motion is modulated by another brain area, such as the paracingulate cortex, which has been implicated in the processing of biological agents rather than artificial agents (Gallagher, Jack,

Roepstorff, & Frith, 2002; Han, Jiang, Humphreys, Zhou, & Cai, 2005; Ramnani & Miall, 2004). There is some evidence that during paradigms hypothesized to tap theory of mind processes, modulation of activity levels in the STS is dependent on whether the participant believes that he or she is interacting with a human or computer opponent (Ramnani & Miall, 2004; Rilling, Sanfey, Aronson, Nystrom, & Cohen, 2004).

Other paradigms lend themselves to testing these new hypotheses. Pozzo, Papaxanthis, Petit, Schweighofer, and Stucchi (2006) have recently demonstrated greater accuracy for determining the end point of a reaching movement dot trajectory (with the final 40% of the movement occluded) if the displayed motion is biologically plausible compared with less biologically plausible motion. The authors suggested that the participants mentally simulated the arm movements to estimate the end points (hence their inaccuracy when the visual stimuli were not biologically plausible). The use of motor processes for this task presumably is dependent on the participant knowing that he or she is observing arm movements. If participants were told that the dot movement was computer generated, we would predict that performance for the two conditions would be equivocal, and this would provide further evidence that the processing of ambiguous movement stimuli as human or artificial can be switched on or off by the viewer's intentional stance, rather than depending on the observed velocity profile per se.

Other experiments on priming of action have suggested that using more schematic stimuli can still prime or inhibit action performance: For instance, schematic images of hands produce similar priming effects to more realistic hand images for both action execution (Press et al., 2005) and visual discrimination during a motor–visual task (Miall et al., 2006, Experiment 5). These results support our findings that the action–observation system in humans can be responsive to a wide range of compatible stimuli.

Brass et al. (2001, Experiment 2) also showed action priming effects for dot motion stimuli that followed the trajectory of their lifting–tapping finger stimulus, although this effect was smaller than the priming effect for observing the actual finger movement. The design of their experiment intermingled trials in which the actual finger movement was presented with trials in which the dot movement was presented. Our own results suggest that Brass et al.'s effect may be due to the participants explicitly associating the dot movement with the finger movement—we predict that performing their priming experiment with all of the dot movement trials first might further reduce the magnitude of the effect for the dot stimuli or remove it completely.

Action Compatibility and Interference

The results of our experiment are compatible with two possible explanations of the interference effect, which correspond nicely to the two main categories of mirror neurons: strictly congruent mirror neurons, which respond to actions depending on effector and muscle groupings (e.g., the muscles involved with moving one's arm from left to right), and broadly congruent mirror neurons, which respond to actions on the basis of goals (e.g., pick up an object) yet whose firing patterns are less concerned with the effector or movement used to achieve that goal (Rizzolatti & Craighero, 2004).

The first source of an interference effect might be quite abstract, wherein the participant may be processing the goal of the actor's movement (e.g., moving the arm to the top position). We suggest that this interference effect manifests as the reported congruency effects. The second source of interference might be more movement specific, wherein the participant may be processing the fine details of the actor's movement (e.g., down to the level of the individual muscles involved). This second type of interference may be behind the impact of motion stimulus error plane variability on movement performance. Evidence from studies looking at involuntary movement induction during observation of action suggest that the effects of perceptual (i.e., stimulus-driven) induction can operate simultaneously with, and independently of, goal-directed induction (De Maeght & Prinz, 2004). This is consistent with the two sources of increased fingertip position variability reported in Experiment 2 (the congruency effect dependent on the agency instruction and the stimulus-variance driven effect that was independent of this factor).

Evidence from developmental studies of action imitation suggest that younger children tend to place more emphasis on imitating the goal of an action rather than on the exact details of effector used: For example, when observing the grasp of an ear that requires using the contralateral hand, many children will use the ipsilateral hand instead (Bekkering, Wohlschlager, & Gattis, 2000). Although it is arguable whether moving one's arm from top to bottom includes a goal per se, it is possible that observing the end state of the movement is the vital aspect of our reported interference, rather than observing the entire movement trajectory. We cannot draw any conclusions on this issue on the basis of our current research, but because the congruency effect for the biological and nonbiological dot motion stimuli was the same (when participants believed they were observing a human agent), it seems viable to suggest that showing the end state of the movement (e.g., a dot that alternates between two positions at left–right or top–bottom) would have a similar interference effect to that reported here for continuous motion.

Reliability of the Interpersonal Interference Effect

It was noted in the discussion for Experiment 1 that participants only showed an interpersonal interference effect when performing a horizontal movement and not during vertical movements. The interaction between performed movement direction and observed movement congruency also approached significance in the original report of this phenomenon by Kilner et al. (2003). For Experiment 2, both groups showed significant main effects of congruency, but one of the groups showed a trend for a stronger congruency effect for the perform vertical movement condition compared with the perform horizontal movement condition, which although not actually significant was in the opposite direction to that found in Experiment 1 and to the trend reported by Kilner et al. (2003).

We interpret these differences in the interpersonal interference effect as being due to the small sample sizes used, rather than to some systematic task difference across experiments. We have performed the same interpersonal interference task in other experiments with identical sample sizes of 10 participants. For one experiment, participants performed the interpersonal interference task alone (Stanley & Gowen, 2006); in the other experiment, we replicated the human-agent instruction condition from Experiment

2, with the dot motion task followed by the interpersonal interference task (Gowen, Stanley, & Miall, 2007). In both sets of data, the main effects of congruency were significant, $F(1, 9) > 10.54$, $p < .011$, whereas the interactions between performed movement direction and congruency were not significant, $F(1, 9) < 2.44$, $p > .153$. These results are consistent with our interpretation of the reported effects of performed movement direction being due to sampling error, rather than to systematic differences introduced by the overall structure of the experimental task. On the basis of the present data, we are unable to draw firm conclusions on the issue of whether interference effects on performed movement are more pronounced for one movement plane compared with the other, and so this question remains open as a topic for future research.

Conclusions

In conclusion, it appears that processing of dot motion stimuli in our experiment depended on the participant's belief about the provenance of the dot trajectories. The interference effect reported by Kilner et al. (2003) is not dependent on the observation of a moving person or on the biological origin of the observed motion trajectory but instead is dependent on whether an observed movement is interpreted as human movement. We suggest that the pathway through which dot motion observation produces the interference effect is the same as that hypothesized to underlie the interference effect during the interpersonal movement task (Blakemore & Frith, 2005; Kilner et al., 2003)—STS processing of the visual properties of the motion, feeding into the ventral premotor cortex, where motor contagion between the conflicting observed and the to-be-executed movements produce a noisier motor output during simultaneous action observation–execution. Both the pathway for the basic interference effect and the areas in which agency may affect the processing of ambiguous movement stimuli still need to be confirmed through neuroimaging techniques.

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