Interaction effects in simultaneous motor control and movement perception tasks

Stuart Jackson · Nuala Brady · Fred Cummins · Kenneth Monaghan

Abstract Recent findings in neuroscience suggest an overlap between those brain regions involved in the control and execution of movement and those activated during the perception of another's movement. This so called 'mirror neuron' system is thought to underlie our ability to automatically infer the goals and intentions of others by observing their actions. Kilner et al. (Curr Biol 13(6):522–525, 2003) provide evidence for a human 'mirror neuron' system by showing that the execution of simple arm movements is affected by the simultaneous perception of another's movement. Specifically, observation of 'incongruent' movements made by another human, but not by a robotic arm, leads to greater variability in the movement trajectory than observation of movements in the same direction. In this study we ask which aspects of the observed motion are crucial to this interference effect by comparing the efficacy of real human movement to that of sparse 'point-light displays'. Eight participants performed whole arm movements in both horizontal and vertical directions while observing either the experimenter or a virtual 'point-light' figure making arm movements in the same or in a different direction. Our results, however, failed to show an effect of 'congruency' of the observed movement on movement variability, regardless of whether a human actor or point-light figure was observed. The findings are discussed, and future directions for studies of perception-action coupling are considered.

Keywords Perception · Action · Mirror neurons · Neuroscience · Biological motion · Motor control

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1 Introduction

Human movement differs from other types of motion stimulus in that human observers typically have experience both producing and perceiving such movement (Shiffrar and Pinto 2002). In fact, the close relationship between produced and perceived movement may also hold at a representational level, as hinted at by the discovery of 'mirror-neuron' systems in primates. Single-cell neurophysiological recordings in macaque monkeys suggest that when the monkey observes the actions of another monkey or human, a pattern of neural activation occurs in the animal's nervous system similar to that motor system activation that occurs when the monkey performs the same action (di Pelligrino et al. 1992; Rizzolatti et al. 1996a). These shared perception-action systems are thought to provide a means for 'action representation' or 'action understanding' (Rizzolatti and Craighero 2004), and more indirect neuroimaging techniques suggest they may also operate in the human nervous system (Fadiga et al. 1995; Rizzolatti et al. 1996b; Grafton et al. 1996; Cochin et al. 1998).

2 Behavioural Studies of observation–execution interaction

If perceived human movement activates the motor system of the observer, it follows that perceived movement may have a role to play in the control of ongoing actions. This idea has been tested using several behavioural paradigms involving simultaneous motor control and movement perception tasks (Brass et al. 2000, 2001; Craighero et al. 1998, 2002; Press et al. 2005; Heyes et al. 2005; Kilner et al. 2003), and relates also to research on the effects of motor task on movement perception (Jacobs and Shiffrar 2005).

Perceived movement is thought to give rise to a kind of 'motor preparation' in the observer—a process of 'automatic imitation' (Heyes et al. 2005) or 'motor contagion' (Blakemore and Frith 2005) occurs, which prepares the observer to execute the observed movement. To test whether movement observation interacts with movement execution, Brass and colleagues (2001) used a stimulus-response compatibility (S-RC) task involving finger movements. The task required one of two types of pre-specified movement from participants following presentation of a cue—either lifting the index finger a set distance off a table and keeping it there, or lifting the finger the same distance and then returning it to rest on the table. The cue to begin each trial consisted of a still image of a hand presented on a monitor—the hand was positioned with the index finger either in the final elevated position, or resting on the table. Participants displayed quicker task performance times when the cue was compatible with the final position of the executed movement. For example, when the participants' task was to lift and then return the finger to the resting position, reaction times were faster when the resting-finger image served as cue than when the elevated-finger image served as cue, suggesting that movement execution is aided when visual stimuli presented immediately preceding the movement are compatible with that movement.

Visuo-motor priming for 'grasping' movements has also been studied extensively by Craighero and colleagues (1998, 2002). In one study, participants were asked to prepare to grasp a bar rotated either clockwise 45° or counterclockwise 45° with respect to their body position. Upon presentation of a cue, which was a mirror image picture of a hand in either the clockwise or counterclockwise grasp position, participants grasped the bar as quickly as possible. The authors found shorter reaction times when "the intrinsic properties of the visual object used as imperative stimulus were congruent with those of the object to be grasped", evidence the authors suggest that there is a tight link between certain visual stimuli and certain motor actions.

3 Biological plausibility of the observed movement

An emerging theme in these investigations is the degree of biological plausibility in the perceptual stimulus—that is, how similar in spatial and temporal characteristics the movement or cuing stimulus is to real human movement—and the effect this has on observation–execution interaction. The assumption is that the more biologically 'plausible' the movement is, the stronger the interaction effects; the less biologically plausible the movement is, the weaker the interaction effects.

A study by Kilner and colleagues (2003) investigated this idea by looking at participants' gross arm movements while simultaneously perceiving arm movements made by either animate or inanimate stimuli. Participants made uniform horizontal and vertical whole arm movements while *at the same time* watching either an experimenter or a robot perform either congruent or incongruent arm movements i.e. in the *incongruent-horizontal-robot* condition, for example, participants made horizontal movements while observing a robot making vertical movements. The researchers found a significant *interference* effect on performance, measured as variance in arm movement, when participants watched the human experimenter perform incongruent arm movements. No interference effect was observed when participants viewed incongruent robotic arm movements. Also no facilitation effects were observed in the congruent conditions, though this may have been a result of the type of gross movement that was studied.

Because interference was only observed in the incongruent experimenter condition, Kilner et al. (2003) suggest that motor control may suffer a small but measurable cost as a result of the *simultaneous* activation of the shared neural systems that underlie movement observation and execution, with a significant effect most probably only evident during observation of *biological* movement and not for non-biological movement. This raises the obvious question of what exact features of biological movement lead to the interference effects seen in the above study and how it is that these features can create a kind of 'motor resonance' in mirror networks. Put more generally, what is it about biological movement that distinguishes it from non-biological movement? Is it the presence of facial and other bodily features, the velocity profile and type or goal of movements, or relative features such as the distances between joints and limb positions, that trigger motor excitation in the observer (Blakemore and Frith 2005)?

Press and colleagues (2005) recently found that robotic movement leads to at least some level of visuo-motor priming. In this study, participants had to perform 'opening' or 'closing' movements of the hand in response to compatible, incompatible or neutral cues. Cues were images of a human hand in either an open, closed, or neutral position, or similar images of robot-like hands. While the human hand stimuli had a stronger effect on performance overall, reaction times were faster following presentation of compatible stimuli than following incompatible stimuli, for both the human and robot cue types. This suggests that the processing of motion information may involve a measure of how human-like the movement is, with robot movements giving rise to some level of mirror activity, on account of them sharing some features of human movement (e.g. limb size and limb division). We should note, however, the difference between stimulus-response pairing tasks (Brass et al. 2000, 2001; Craighero et al. 1998, 2002; Press et al. 2005) and on-line movement observation-execution tasks like that used by Kilner et al. (2003). A particular strength of both types of task is their focus on low or even single dimensional movements. However, comparing findings from one type of study to the other may require that consideration be given to the stage of action processing at which interaction effects occur—for static cue tasks, interaction may occur transiently around the

action planning stage, while for dynamic on-line perception-action tasks, interaction may occur throughout the action cycle.

A stimulus type used in much contemporary research on human movement perception and that may be useful where control of the 'biological plausibility' of observed movement is needed, is the *point-light display*. These biological motion stimuli consist of points of light representing the main joints of an actor engaged in movement, and can be constructed in one of several ways—by placing small lights on the joints of the actor and videotaping the actor moving in a darkened room (Johansson 1973); using specially devised algorithms that model the locations and motions of joints (Cutting 1978); using data obtained from 3-D motion capture equipment, rendered using animation or graphical software (Troje 2002; Ma et al. 2006) (for a detailed review of the various methods of point-light construction see Dekeyser et al. 2002). Point-light displays provide not only an ideal complement to observation of real human movement, but provide a useful and manipulable lab-based resource.

An interesting question in the current context is whether point-light recordings of real human movement contain enough information to interact with on-line movement control. The majority of research with point-light displays has so far focussed on the viewer's ability to extract cues for such qualities as gender, identity or even affect of the moving actor (Mather and Murdoch 1994; Troje 2005; Pollick et al. 2001). Information relating to constraints on body movement, such as the weight of a lifted box or the weight of a thrown object, can also be extracted from point-light sequences (Runeson and Frykholm 1981, 1983). More recently, researchers have used point-light displays to study the link between action observation and action execution. A comprehensive series of studies by Jacobs and Shiffrar (2005) tested the effects of concurrent motor activity on perceivers' sensitivity to human movement depicted in point-light displays. During one of three different motor tasks (walking on a treadmill, cycling, standing-still) participants had to judge which of two simultaneously presented point-light walkers walked faster. Participants who engaged in walking showed the least sensitivity to speed differences in the observed walkers. Participants engaged in cycling, however, had a similar level of performance on the speed discrimination task as stationary observers, ruling out a dual-task interference explanation of the findings. It appears that perception and performance of the same movement alters regular visual-motion processes (Jacobs and Shiffrar 2005). If this visuo-motor link is responsible for the effects of current motor activity on perception of movement represented in point-light displays, then could the relationship hold in the opposite direction? Would real human movement represented in point-light displays interact with on-line movement control?

4 Current study

The current study investigates the interaction effects of observed human movement on simultaneous movement control using two categories of perceptual stimulus—a real human actor and a moving 'point-light' actor. In line with recent behavioural and neuroimaging investigations of shared perception-action systems (Kilner et al. 2003; Sakreida et al. 2005; Wheaton et al. 2004), we used intransitive, goal-free body movements as the observed movement stimulus—a person holding their right arm at shoulder height and moving it at a steady pace forward and back or up and down. The motor control task involved the same type of goal-free, arm movement.

By manipulating the direction and congruency of the simultaneously observed and performed movements so that on some trials a movement congruent with the performed movement was observed and on other trials an incongruent movement was observed, we

Table 1 The 10 conditions studied in the experiment

	Human congruent	*Human incongruent*	*Point-light congruent*	*Point-light incongruent*	*Control*
Horizontal	2 trials	2 trials	2 trials	2 trials	2 trials
Vertical	2 trials	2 trials	2 trials	2 trials	2 trials

The row headings correspond to the movement made by participants on any particular trial while the columns detail whether a human or virtual figure was observed, and whether the observed movement was the same as (congruent) or different than (incongruent) the movement simultaneously executed. There was no observation task for the control conditions. Two trials were carried out for each condition

hoped initially to replicate the findings of Kilner et al. (2003) of interference in movement accuracy while observing an incongruent or incompatible movement made by another human. A facilitation effect was not found in the previous study and was not explicitly hypothesised here, although the possibility that observing compatible movements might lead to more accurate movements (i.e. less variable movements) than in control trials was not ruled out. Considering the growing evidence highlighting the effectiveness of point-light stimuli in modelling real human movement, for point-light observation conditions we hypothesised a relationship matching with any interaction effects found for observing real human movement. As this is the first study we are aware of to test the effects of observing moving point-light stimuli on simultaneous movement control tasks, the possibility remains that a different profile of interaction effects may occur. A reduced or enhanced interference effect may arise, or perhaps a facilitation effect may occur while observing congruent point-light stimuli.

5 Method

5.1 Participants

Eight participants performed the current task (six male, age range 17–36, mean 21.8 years). All were right-handed and had normal or corrected-to-normal vision. Biometric data was obtained for all participants—height, weight, and arm length. All gave informed consent, and the study was carried out with the approval of the Research Ethics Committee at UCD.

5.2 Task

Participants carried out simultaneous movement performance and movement perception tasks. In each trial, whole arm movements in either a horizontal (forward and back) or vertical (up and down) direction were simultaneously performed and observed for a duration of 20 s. Movements were not mixed in any trial i.e. if the participant began making horizontal movements in any trial, he/she continued to make horizontal movements until the trial was complete. The observed movement, however, could differ from the movement performed; this was manipulated so that on half of the trials the observed and executed movements were the same as each other and on the other half they were different.

The 10 conditions are outlined in Table 1. In the *Horizontal—Human Congruent* condition, for example, a trial consisted of the participant making sinusoidal horizontal arm movements while simultaneously watching the experimenter making the same movements, that is, congruent horizontal movements. In the *Vertical—Point-light Incongruent* condition,

for example, participants made sinusoidal vertical arm movements while simultaneously watching the point-light figure making horizontal movements (projected onto a screen). In *Control* conditions, participants made arm movements in the absence of any observed movement. Two trials were carried out in each condition and trials were performed in random order. The participant was instructed on what type of movement to make before each trial, horizontal or vertical, and told what type of actor would be observed (human actor, point-light figure, control). The participant did not receive information on whether the observed movement would be congruent or incongruent with his/her own movement.

Before each trial the experimenter gave a 'Ready' signal to the participant. After 3 s the human actor/point-light figure began the movement, which served as the participants cue to begin his/her movement. In control conditions, the experimenter followed the 'Ready' signal 3 s later with a 'Go' signal. The experimenter carried out the movement that was observed during the 'human actor' observation trials, and was blindfolded during these trials. All movements were carried out with the right arm, and began with the arm held at comfortable shoulder height with the palm facing forward. Horizontal movements began with the arm moving forward first and then back. Vertical movements began by moving upwards first and then down. Movements then continued in the respective planes until 20 s of recording was completed. This was signalled by a beep from the tracking device. Participants rested between each trial.

Participants were instructed to make straight-arm movements in either the vertical or horizontal plane, while maintaining fixation on the hand of either the human actor or point-light figure during the trials. Participants were also instructed to move in time with the observed movement. Instructions were also given to minimise torso movement during the trials, and to maintain an evenly weighted stance throughout. The experimenter/point-light figure was situated 2.5 m from the participant during trials.

5.3 Stimulus design

For the 'Human' observation conditions, the participant observed the experimenter performing either vertical or horizontal arm movements depending on the trial. For the 'Point-Light' trials, the participant observed recordings of real human movement represented as points of light moving on a screen. These 'point-light' stimuli were created from recordings of horizontal and vertical arm movements made by the experimenter before testing. Recording was carried out in the Movement Analysis Lab in the School of Physiotherapy and Performance Science, UCD, using the CODA 3-D Motion Analysis System (Charnwood Dynamics, Leicestershire, U.K.). Thirteen LED markers were attached to the main joints of the body (ankle, knee, hip, wrist, elbow, shoulder) and the forehead, and the position of these markers relative to a common reference frame was then monitored and recorded by the tracker. The coordinate data obtained from these recordings was then extracted and any irregularities smoothed before transfer into Matlab for stimulus creation. Individual frames of the movement sequences were plotted in Matlab and an *.avi* file was created from the individual frames using VirtualDubMod software (http://www.virtualdub.org). Frame rate was set to 50 Hz, and the stimuli were projected onto a screen, with size analogous to the human actor (approx. 5' 10" in height), using a Hitachi CP-X325 LCD projector. The figures appeared as white dots on a black background, with an orientation directly facing the participant. Figure 1 above shows a series of frames from one of the two stimuli used in the study, showing vertical arm movement.

Fig. 1 A selection of frames (not in sequence) from the vertical 'point-light' stimulus, created with coordinate data from real movement recordings plotted in Matlab. When projected onto a screen the figure appeared with height analogous to the human actor (5'10" approx.)
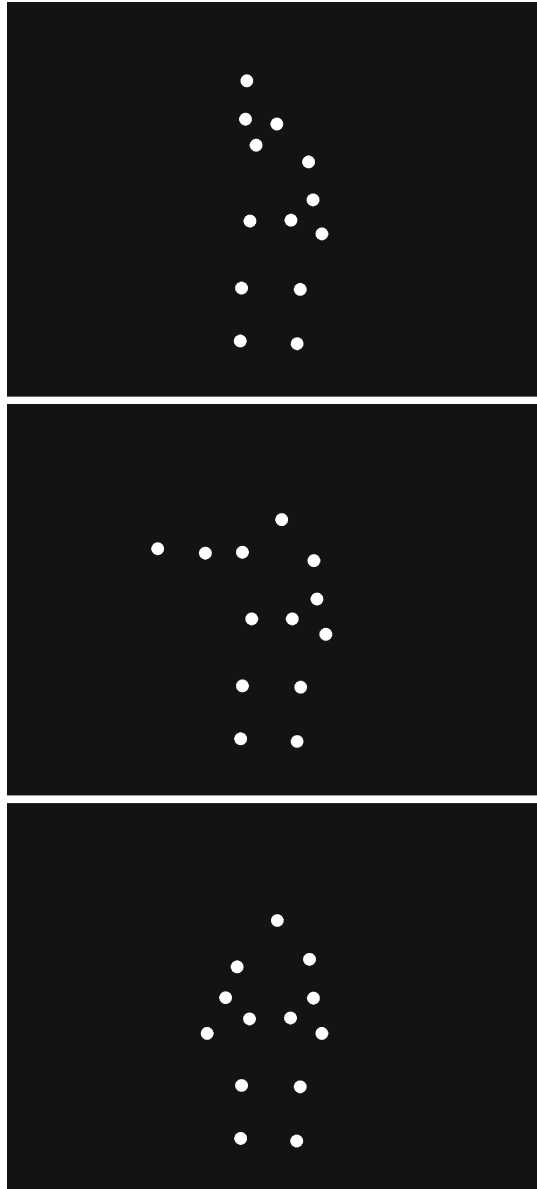
5.4 Movement recording

Participants' movement was recorded using the same 3-D motion tracking equipment as used in the stimulus design phase. Following introduction and biometric data measurement, participants were given the chance to practice observing and simultaneously executing the horizontal and vertical arm movements in the different conditions. This familiarised participants with the task and the movement velocity of the observed stimuli, which was set at approximately 0.7 Hz or 14 full arm movements during the 20 s of recording. Pilot data had

suggested that point-light stimuli with slower movement rates were difficult for participants to maintain a rhythm with and sometimes led to task confusion. Six LED markers were then attached to the participant's right arm and upper torso at the following locations—sternal notch, 3 cm below sternal notch, coracoid process (shoulder), elbow, wrist, tip of middle finger. Movement was recorded at a rate of 100 Hz for each of these points during the twenty trials.

6 Data analysis

6.1 Visualising the movement space—transformation from cartesian to spherical coordinates

The variable of interest in the current study was the variance of the executed movement in the plane *orthogonal* to the main movement direction. However, as the sample horizontal trial in Fig. 2a and b illustrates, the main movement direction can be decomposed into primary and secondary components, that is movement along the *x*- and *y*-axes, respectively for horizontal trials (and movement along the *z*- and *y*-axes, respectively for vertical trials). The hand position data from the raw movement recordings was therefore referenced to the shoulder position before being transformed from Cartesian ⟨x,y,z⟩ coordinates to spherical ⟨theta, phi⟩ coordinates, using the standard transforms:

$$\theta = \arctan(y/x)$$
$$\o = \arctan(\sqrt{(x^2 + y^2)}/z)$$

Figure 2c illustrates the transformation for this horizontal trial. Movement in the 3-dimensional ⟨x,y,z⟩ coordinate space is reduced to movement in a 2-dimensional ⟨theta,phi⟩ coordinate space, representing the angular displacement of the finger coordinate over time relative to the shoulder coordinate. Position along the *x*- and *y*-axes is effectively combined into a single value, *theta*, with position orthogonal to this main direction represented by *phi*.

6.2 Statistical Analysis

Ten full sweeps forwards and backwards (horizontal trials) or upwards and downwards (vertical trials) were analysed from each trial, and the mean across both trials for each condition was taken for each subject. A normal probability plot highlighted skewness at the upper bound of the data; scores were thus log transformed and a $2 \times 2 \times 2$ repeated measures analysis of variance was carried out on the data, looking at the three factors of congruency (Congruent versus Incongruent), effector (Human actor versus Point-Light figure) and direction (Horizontal versus Vertical).

None of the main effects were significant (congruency: df $= 1,7$; $F = 0.35$; $P > 0.5$; direction: df $= 1,7$; $F = 0.63$; $P > 0.1$; effector: df $= 1,7$; $F = 2.42$; $P > 0.1$). None of the interactions reached statistical significance either (congruency × effector: df $= 1,7$; $F = 2.08$; $P > 0.1$; congruency × direction: df $= 1.7$; $F = 0.26$; $P > 0.5$; effector × direction: df $= 1,7$; $F = 0.106$; $P > 0.5$; congruency × effector × direction: df $= 1,7$; $F = 0.602$; $P > 0.1$). A further analysis was performed on individual movement segments. Data from each trial was segmented into movements forwards and backwards or upwards and downwards, thus giving 20 separate segments per trial. The variance of each segment in the plane orthogonal to the main movement direction was calculated, and the mean across both trials of each condition obtained. A repeated measures analysis again failed to find a significant main
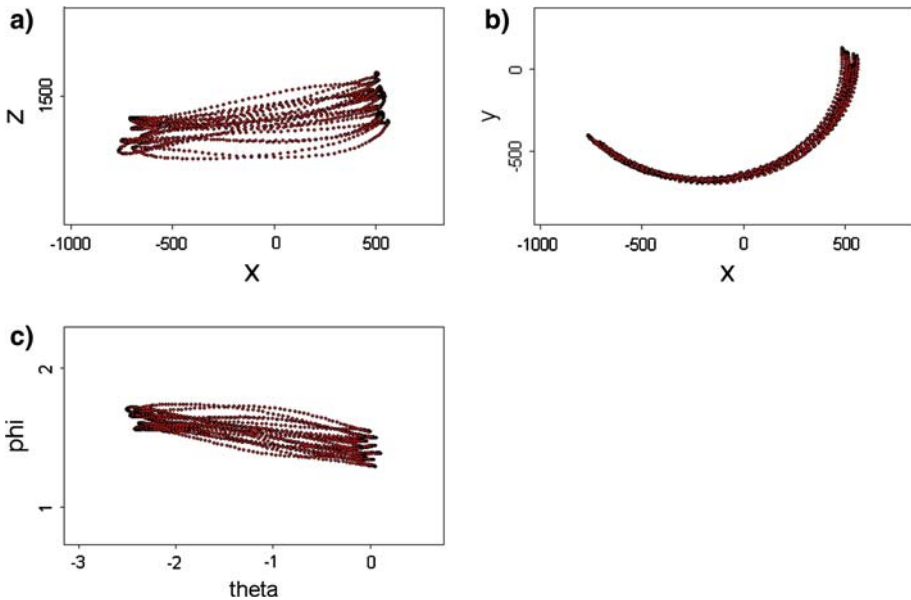
Fig. 2 Visualising and analysing a sample horizontal trial, containing ten arm movements forwards and backwards: **(a)** and **(b)** By visualising the raw ⟨x,y,z⟩ hand-position coordinate data, we can see that the main movement direction varies primarily along the *x*-axis, with a secondary component along the *y*-axis **(c)** The two horizontal components are therefore combined using a Cartesian—Spherical coordinate transform, with shoulder position taken as a dynamic origin. This reduces the 3-dimensional ⟨x,y,z⟩ space into a 2-dimensional ⟨theta,phi⟩ coordinate space. The variance of *phi* for each trial is then taken as a measure of interaction effects. Note that ⟨x,y,z⟩ are measured in millimetres, ⟨theta,phi⟩ in radians

effect for congruency (df $= 1,7$; $F = 0.034$; $P > 0.5$). The other main effects were also not significant—effector (df $= 1,7$; $F = 2.501$; $P > 0.1$), direction (df $= 1,7$; $F = 2.048$; $P > 0.1$). A small but significant interaction was found for congruency $\times$ effector (df $= 1,7$; $F = 5.96$; $P < 0.05$) and effector $\times$ direction (df $= 1,7$; $F = 7.96$, $P < 0.05$); the other interactions were not significant – congruency $\times$ direction (df $= 1,7$; $F = 2.029$; $P > 0.1$), congruency $\times$ effector $\times$ direction (df $= 1,7$; $F = 0.014$; $P > 0.5$). However, paired *t*-tests showed that none of the congruency $\times$ effector conditions were significantly different from baseline - human congruent $\times$ baseline ($t = 0.43$; $P > 0.5$), human incongruent $\times$ baseline ($t = 0.5001$; $P > 0.5$), point-light congruent $\times$ baseline ($t = 0.3$; $P > 0.5$), point-light incongruent $\times$ baseline ($t = 1.274$; $P > 0.24$); thus any differences between the four test conditions themselves may have been misleading. A closer look at the overall trial means in Fig. 3a and b is helpful in understanding the data. Each of the four congruency-effector conditions (human congruent (C-HU), human incongruent (I-HU), point-light congruent (C-PL), point-light incongruent (I-PL)) overlaps to a large degree with each of the others, and none is significantly different than baseline. Interestingly, outlier data does appear more common in the 'observation' conditions than in the 'no observation' control condition. Collapsing across all conditions and looking at the subject data individually, we can see that the range of scores varies some extent across subjects.

With no conclusive main effects, the study hypotheses cannot be supported. The clear lack of a significant interference effect for observed incongruent human movement was surprising as this went against the results of Kilner et al. (2003) and results from other
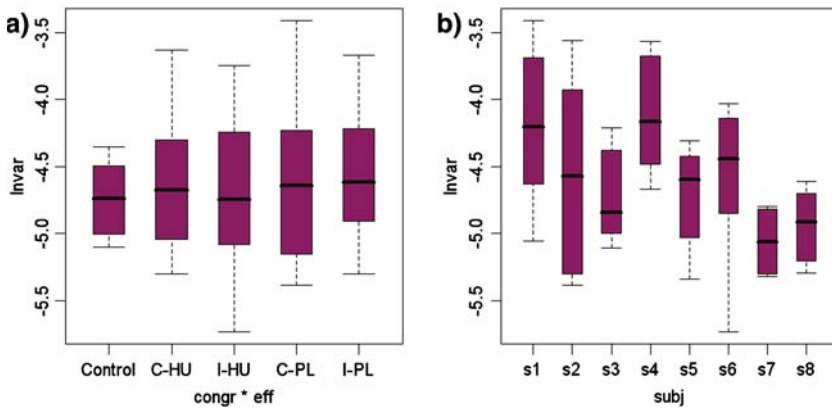
Fig. 3 (a) Mean of the log transformed variance in each of the congruency × effector conditions, collapsed across direction and subjects. **(b)** Analysis of the subject data collapsed across all conditions highlights large interindividual variability

previous perception-action studies (Brass et al. 2001; Craighero et al. 2002; Press et al. 2005; Heyes et al. 2005).

7 Discussion

The current study failed to replicate a significant interference effect of observed incongruent human movement on simultaneously performed movements. This goes against previous research findings and needs to be considered. In addition, the study failed to find significant interaction effects of observed point-light movement on simultaneous motor activity. This is less surprising as no previous study we are aware of has tested this hypothesis. These findings will now be discussed in relation to previous perception-action research, and future directions for such studies will be considered.

Why might observing a real human actor simultaneously engaged in goal-free arm movements not interact with one's performance of similar goal-free arm movements? If observing a movement primes the observer to carry out a similar movement, and makes the performance of incompatible movements more computationally effortful, as suggested by a large amount of previous work (Brass et al. 2001; Craighero et al. 2002; Press et al. 2005; Heyes et al. 2005; Kilner et al. 2003), then we could have expected the observed incongruent human movements to interfere more with simultaneous motor activity than the observed congruent movements. Previous work by Kilner et al. (2003) using a similar task had found a significant interference effect where the observed human movement was incongruent with the executed movement. Incongruent robotic movement, in contrast, failed to have the same effect. In addition, Press et al. (2005) found that a crucial variable in mediating perception–action interaction was the degree of biological plausibility of the observed movement, which a human actor could be expected to typify. This prediction, however, wasn't confirmed in the current study. The analysis found that variability in motor performance while observing real human movement did not significantly differ from baseline, regardless of whether the perceived movement was congruent or incongruent with the observer's current motor activity.

One possible reason why observing a human actor failed to interact significantly with movement performance in the current task might be that task or method specific effects

resulted in less interaction between the observed human movement and on-line arm movement control. Could task demands have resulted in reduced interference while observing the real human actor? Previous research suggests that mirror system activation can be modulated by attentional demands. Asking someone to observe a movement for the purpose of later imitation will lead to different activation than if the same movement is passively observed (Iacoboni et al. 1999). The current task required participants to fixate on the hand of the human actor while simultaneously performing a movement. The task was one of visual fixation rather than imitation; on half of the trials the participants' and actor's movements in fact differed. However, this passive fixation was similar to that used by Kilner et al. (2003), and therefore a similar interference effect for observed incongruent human movement could have been expected.

One feature of the task that did differ from that used by Kilner et al. (2003) and that may explain the failure to replicate the significant interference effect was the rate at which the observed and executed arm movements were performed. Several participants in the pilot study had found it difficult to keep in time with point-light displays depicting arm movement at a rate of 0.5 Hz (10 full sweeps in 20 s), commenting that this rate of movement felt unnaturally slow. A quicker rate of movement (0.7 Hz, 14 full sweeps in 20 s) was therefore used for both the point-light and human observation conditions. Perhaps even more crucially, the extent of arm movements in the current task was greater than that used by Kilner et al. (2003). Subjects in the current study were instructed to move as far as *was comfortably possible* in each of the respective directions, which led, in horizontal trials for example, to several subjects approaching as far forward as the midline during the forward movement, and as far back as 45°s from their shoulder line in the backward part of the movement. A more constrained movement extent may have revealed more clearly any interaction effects.

The possibility that observed human movement failed to interfere with simultaneously executed movement because of a lack of significant motor system activation following movement observation cannot be ruled out. The distinction between observing goal-directed actions, and observation of goal-free, intransitive movements (like the movements used in the current study), may be instructive here. The idea that mirror-neuron systems encode specific 'actions', 'goals', or 'intentions' has been suggested by several researchers (Jeannerod 1994; Rizzolatti and Craighero 2004; Lyons et al. 2006). Could it be the case that the goal-free, intransitive tasks used in the current study don't engage mirror networks *exactly because* they lack real 'action' or 'intention' content? A growing number of functional imaging studies have shown motor system activation following observation of movements not involving any explicit goal (Buccino et al. 2001; Wheaton et al. 2004; Sakreida et al. 2005). In one study, participants observed mouth opening/closing, hand opening/closing and leg movements forwards and backwards (Wheaton et al. 2004). Group data highlighted several centres of activation—aside from MT/V5 activation to all types of motion, selective activations were seen that involved the STS, ventral premotor cortex, and anterior intraparietal (aIP) cortex, the last two regions of which are central parts of the motor system and generally considered part of the mirror system. In another recent fMRI study, Sakreida and colleagues (2005) found premotor cortex activity during a task in which participants had to tell whether moving body parts were accelerating or decelerating.

Thus it seems unlikely that observing goal-free body movements like those used in the current task gives rise to no activation in motor systems. Rather the amplitude of activation resulting from observing the human actor in the current task may have been below a level sufficient to interfere with online movement control. This may have been caused by several aspects of the current method, in particular the extent of performed arm movements, which as noted, may not have been constrained enough. Tasks need to be developed where

'embodiment' by the observer of the observed 'intransitive' action can be more clearly controlled. Forced choice acceleration/deceleration or speed discrimination tasks (Sakreida et al. 2005; Jacobs and Shiffrar 2005) may go some way to achieving this.

The question remains open as to whether movement represented in point-light displays contains enough information to interact with on-line motor control. A large body of research has shown that movements depicted by a small number of dots representing the main joints of an actor are effective in conveying perceptually relevant information (Johansson 1973; Cutting 1978; Mather and Murdoch 1994; Troje 2005; Pollick et al. 2001). In addition, the fact that the perception of movement depicted in point-light displays can be altered by simultaneous motor tasks has previously been shown (Jacobs and Shiffrar 2005). The current study, however, failed to show that the opposite pattern holds—that is, that observing movement represented in sparse, point-light displays interacts with the observer's current motor activity. The same methodological limitations that affected the human observation conditions, such as the extent of the performed movements, might also have played a role here. Future studies need to employ more constrained task conditions with larger subject groups.

If observation of movement in point-light displays could be shown to interact with online motor control, it would be interesting because it would suggest that those aspects of observed human movement necessary to activate the motor system of the observer are retained in point-light displays of real human movement. The visual presence of facial features or real body parts might be shown to be unnecessary for the perceived movement to have an effect on the observer's motor system. This might have relevance for areas of research such as motor rehabilitation (Stefan et al. 2005; Holden and Dyar 2002) and autism (Oberman et al. 2005). For example, the provision of virtual 'teacher' movement and subsequent performance feedback has been shown to enhance recovery in patients with impaired upper limb use resulting from stroke (Holden and Dyar 2002). The grounds for believing that kinematic and dynamic aspects of movement isolated by point-light displays may be sufficient for observation–execution matching are reasonably firm. Perceivers can not only obtain motion-mediated structural cues from point-light displays (Troje 2002), but can also infer dynamic aspects of the actor's movements, such as force, momentum, or even 'intention' from the kinematic information available in the display (e.g. velocity, acceleration) (Runeson and Frykholm 1981, 1983). Coupled with the fact that human movement naturally obeys certain constraints regarding speed and trajectory (Viviani and Stucchi 1992; Flash and Hogan 1985), the possibility that real human movement represented in point-light displays could trigger observation-execution 'mirror' systems seems likely.

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