Title: Motor contagion: the contribution of trajectory and end-points

Running head: Trajectory and end-points

James W. Roberts[*], Spencer J. Hayes, Makoto Uji, Simon J. Bennett

Brain and Behaviour Laboratory,
Liverpool John Moores University, Liverpool, UK

[*]Corresponding author
Brain and Behaviour Laboratory, Faculty of Science, Liverpool John Moores University,
Byrom Street, Liverpool, L3 3AF, UK
Tel: +44 (0) 151 904 6237, Fax: +44 (0) 151 904 6284
J.W.Roberts@2006.ljmu.ac.uk

Abstract

Increased involuntary arm movement deviation when observing an incongruent human arm movement has been interpreted as a strong indicator of m*otor contagion*. Here, we examined the contribution of trajectory and end-point information on motor contagion by altering congruence between the stimulus and arm movement. Participants performed cyclical horizontal arm movements whilst simultaneously observing a stimulus representing human arm movement. The stimuli comprised congruent horizontal movements or vertical movements featuring incongruent trajectory and end-points. A novel, third, stimulus comprised curvilinear movements featuring congruent end-points, but an incongruent trajectory. In Experiment 1, our dependent variables indicated increased motor contagion when observing the vertical compared to horizontal movement stimulus. There was even greater motor contagion in the curvilinear stimulus condition indicating an additive effect of an incongruent trajectory comprising congruent end-points. In Experiment 2, this additive effect was also present when facing perpendicular to the display, and thus with end-points represented as a product of the movement rather than an external spatial reference. Together, these findings support the theory of event coding (Hommel et al., 2001), and the prediction that increased motor contagion takes place when observed and executed actions share common features (i.e., movement end-points).

Keywords

Motor contagion; mirror system; observation-execution; trajectory; end-points

Introduction

It is well accepted that there is a close link between perception and action, and accordingly this has been recognised in numerous conjectures on the processes involved in action-observation: common-coding (Prinz, 1997), theory of event coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001) and direct-matching (Rizzolatti, Fogassi, & Gallese, 2001). Indeed, the discovery of so-called mirror neurons within the premotor cortex of the monkey, which are activated during the observation and execution of a reach-and-grasp action, provides neurobiological evidence to substantiate the commonality between perception and action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). A similar mirror system was subsequently identified within the fronto-parietal regions of the human brain (Cattaneo, Sandrini, & Schwarzbach, 2010; Hamilton & Grafton, 2006; Iacoboni et al., 1999), and was postulated to have several behavioural consequences for action understanding and social imitation (Boria et al., 2009; Chartrand & Bargh, 1999). For instance, automatic imitation predicts that faster response times are made when a stimulus onset cue corresponds with the pre-requisite movement response (e.g., a background image of an index finger movement accompanying an index finger movement response; Brass, Bekkering, Wohlschläger, & Prinz, 2000). In a similar vein, individuals performing an interpersonal observation-execution task exhibit involuntary orthogonal arm movement deviation during the observation of incongruent, as opposed to congruent, human arm movements (Kilner, Paulignan, & Blakemore, 2003). The latter effect has been referred to as *motor contagion* (Blakemore & Frith, 2005), and is thought to occur when the observed human stimulus activates an internal representation that interferes with the efferent motor commands generated by the observer.

There have been attempts to determine the stimulus (Hardwick & Edwards, 2012; Kilner, Hamilton, & Blakemore, 2007) and contextual (Stanley, Gowen, & Miall, 2007) properties underpinning motor contagion. For example, Hardwick and Edwards (2012) suggested that contagion results from incongruent spatial direction (lateral vs. anterior) when performing an incongruent goal-directed action (horizontal flexion-extension of the shoulder vs. flexion-extension of the elbow). Similarly, it has been suggested that arm movement deviation associated with incongruent stimuli may be influenced by the incongruent end-points, as opposed to the trajectory (Gowen, Stanley, & Miall, 2008; Stanley et al., 2007). The implication is that motor contagion, like several other behavioural effects during action-observation, may be mediated by a mirror system comprising multiple levels of action-representation (Csibra, 2007; Grafton & Hamilton, 2007; Wohlschläger, Gattis, & Bekkering, 2003).

While not intending to debate the findings of previous empirical or theoretical work on motor contagion, to date, no single study on motor contagion has directly examined the combination of observed trajectory and end-point information on the executed action. In this respect, it is notable that although Stanley et al. (2007) reported that motor contagion may be related to the incongruent movement end-points, in the same study they found increased deviation during the observation of biological compared to non-biological motion, irrespective of the congruency of movement direction. The authors suggested this was a result of the inherent variability in the observed biological motion, and thus a source of bottom-up interference related to the trajectory. Thus, our aim was to examine the contribution of trajectory and end-point information on motor contagion. Specifically, we aimed to determine the effect of congruence between the executed action and the trajectory and/or end-point features of the observed stimuli. Importantly, to minimize the influence of top-down factors, such as human form (Kilner et al., 2007; Press, 2011; Stanley et al., 2007), we presented the stimuli as a non-human agent with biological motion properties.

Experiment 1

Introduction

Using a similar experimental design to that of Stanley et al. (2007), here we required participants to perform cyclical horizontal arm movements across the mid-line of their body whilst observing a moving dot stimulus representing pre-recorded human arm movement. Two of the conditions of observed stimuli included horizontal movements similar to that performed by the participant, or vertical movements featuring incongruent trajectory and end-points. An additional stimulus was generated that displayed a curvilinear trajectory, and thus featured movement end-points congruent with the executed action, but an incongruent trajectory.[1]

It was hypothesised that if observed stimuli are primarily coded as a function of their end-points, limited deviation in orthogonal movement, and thereby motor contagion, would be present in the horizontal or curvilinear conditions. However, if motor contagion is mainly a result of incongruence between the executed action and observed trajectory, it can be hypothesised that there would be increased deviation in both the vertical and the curvilinear conditions. Alternatively, if both of the action features are coded and act in combination to influence motor contagion (Hommel et al., 2001), it follows that movement deviation exhibited in the curvilinear condition will differ from that of the vertical stimulus condition. More specifically, if the coding of the observed incongruent action features elicits increased motor contagion due to similarities with the executed action features then we would anticipate an additive effect when observing the curvilinear stimulus.

In addition to the standard measure of motor contagion, we also sought to determine the mapping of stimulus-motion properties by measuring the spatial congruence between the observed and executed movement. The idea was to attribute any deviation in the participants' movement to the unfolding trajectory of the observed stimuli (Dijkerman & Smit, 2007;

Hardwick & Edwards, 2011). To this end, we calculated the mean peak position over a number of cycles within the orthogonal y-axis. Notably, this dependent measure was much larger for the curvilinear movement than the horizontal and vertical movement (for an explanation see Method). Thus, if the deviation in participants' movement were attributed to the stimulus-motion properties, we would expect participants to exhibit a higher mean peak position in the curvilinear condition than the vertical and horizontal conditions.

Method

Participants

Data was recorded from seventeen participants (aged between 18 to 21 years). All had normal or corrected-to-normal vision and gave written informed consent prior to taking part. The experiment was designed in accordance with the Declaration of Helsinki and was approved by the local ethics committee of the host university.

Stimuli

The visual stimulus was a red circle (1.8 cm) displayed on a flat white screen (2.0 x 1.7 m) at a viewing distance of 1.9 m. The stimulus was generated on a host PC (Dell Precision 670) using the COGENT toolbox implemented in MATLAB (Mathworks Inc), and was displayed using a CRT projector (Barco Graphics 908) with a spatial resolution of 1024 x 768 pixels and refresh rate of 85 Hz. The stimulus reflected 30 s of pre-recorded, scaled data from the moving arm of a volunteer. The movements were well practised in order that the required amplitude and frequency of 1 Hz could be reliably achieved. Scaling of the stimulus was applied in order that 400 mm horizontal displacement in the recorded data corresponded to either 400 mm horizontal or vertical displacement on the projection screen. The movement stimuli consisted of cyclical horizontal and vertical arm movements. In addition, participants were shown a cyclical curvilinear moving stimulus that displaced 400 mm in the horizontal axis and 200 mm in the vertical axis (from centre to the upper vertex). Thus, the curvilinear movement end-points aligned with those of the horizontal stimulus (see Fig. 1). Finally, we included a control condition in which a single red dot was presented at screen centre for the duration of the trial. Participants were instructed to fixate on the stationary stimulus while moving their arm at 400 mm horizontal amplitude. No instructions were given to participants regarding the animacy of the moving stimulus.

Insert Fig. 1 about here

Task and Procedure

Participants were instructed to perform 400 mm amplitude horizontal arm movements across the mid-line of their body in time with a cyclical moving stimulus (or fixating on a stationary stimulus) observed on the projection screen. The room was otherwise dark and participants did not have any external cues regarding the location of the stimulus relative to the screen edge and thus movement reversal. Initially, each participant performed two practice trials with the guidance of stationary targets located 400 mm apart in the horizontal axis and an auditory metronome. Participants were instructed to time their movement so that the end-points, and thus reversals, coincided with the tones. Following practice, the stationary targets and auditory metronome were removed, and participants completed a trial in the control condition. Next they completed two trials in each of moving stimulus conditions, which were randomly ordered with the caveat that no condition could be repeated consecutively. Finally, they completed a second trial in the control condition. The control condition was presented as the first and last trials in order to determine if there were attentional and fatigue effects.

Data collection and analysis

The position of an active infrared sensor attached to the tip of the index finger was recorded at 200 Hz using a 3D Investigator Motion Capture System (Northern Digital Inc., Ontario, Canada). Following data acquisition, the first and last 5 s of data recording were discarded in order to minimize asynchrony around movement onset and potential attentional and fatigue effects (Hardwick & Edwards, 2012). The remaining position data were then filtered at 10 Hz using an autoregressive filter implemented in MATLAB. The same routine next determined individual movement segments by identifying reversals in fingertip position of the dominant movement axis (i.e., x-axis; horizontal). For each movement segment (i.e., a half cycle) the standard deviation of fingertip position within the orthogonal movement axis (i.e., y-axis; vertical) was calculated to provide a measure of motor contagion. The average deviation across movement segments within a trial was calculated for each participant. In addition, the mean peak position within the orthogonal axis was calculated to provide a measure of mapping the stimulus-motion properties. Peak position was determined as the extreme most position within the orthogonal axis of each horizontal movement segment relative to onset, and thus could occur in either the upward or downward direction.

If there were mapping of the stimulus-motion properties to the participant’s movement, it can be expected that movement deviation would occur primarily in the upward direction with the curvilinear stimulus (Fig. 1f), thus leading to a high mean peak position. Looking at the vertical stimulus (Fig. 1e), it can be seen that there is deviation away from the horizontal axis in the upward direction in one segment (positive) and downward direction in the following segment (negative). Involuntary mapping of this motion by the participants would lead to a lower mean peak position due to combining positive and negative deviation from each segment of the movement cycle. For the horizontal stimulus there is very little movement in the orthogonal axis, and thus mapping should result in a similarly low mean peak position.

A paired-samples t-test on average deviation data was first used to compare the control trials. Then, to determine the effect of end-point and trajectory information on participants arm movements, the average deviation and peak position data were submitted to separate one-way repeated-measures ANOVA. Mauchly's test of Sphericity confirmed no significant violation of the equal variance of differences assumption ($p > .05$). Significant effects were decomposed using Bonferroni post hoc procedure ($p < .05$).

Results and Discussion

For the comparison of control trials, there was no significant difference between participants' movement deviation in trial 1 ($M = 6.09$; $SE = .65$) and trial 2 ($M = 7.00$; $SE = 1.38$), $t(16) = .62$, $p > .05$. Thus, there were no significant attentional or muscular fatigue effects introduced by performing the six 30-second duration experimental trials.

ANOVA on average deviation data revealed a significant main effect of stimulus, $F(2, 32) = 15.79$, $p < .001$, partial $\eta^2 = .50$ (Fig. 2). Post hoc comparisons indicated lower movement deviation in the horizontal compared to the vertical ($p < .05$) and curvilinear ($p < .001$) conditions. In addition, average deviation was significantly greater in the curvilinear condition compared to the vertical condition ($p < .05$). The source of these effects can be visualised in Fig. 3, which shows more vertical displacement over movement segments for the vertical condition (Fig. 3b) compared to the horizontal condition (Fig. 3a), and yet even greater displacement for the curvilinear condition (Fig. 3c). Indeed, the participants' movement profile in the curvilinear condition was comparable to the observed curvilinear stimulus (Fig. 1f).

Insert Fig. 2 and 3 about here

For the analysis of peak position, ANOVA revealed a significant main effect of stimulus, $F(2, 32) = 12.15$, $p < .001$, partial $\eta^2 = .43$ (Fig. 4). Post hoc comparisons indicated a significant lower peak position in the horizontal condition compared to the vertical ($p > .01$) and curvilinear conditions ($p > .01$). In addition, peak position in the curvilinear condition was significantly higher than in the vertical condition ($p < .05$). As can be seen in Fig. 3c, peak position in curvilinear condition was reflective of the primary upward movement for both left (*black trace*) and right (*grey trace*) movement directions of the curvilinear stimulus. However, when observing the vertical stimulus, participants moved mainly upwards in one segment (*black trace)* and downwards (*grey trace*) in the following segment, thus leading to peak position closer to zero.

Insert Fig. 4 about here

Consistent with previous work (Kilner et al., 2003; 2007), we found evidence of motor contagion during the observation of a vertically-moving stimulus, and thus incongruent trajectory and end-points. There was even greater motor contagion when participants observed the curvilinear stimulus. Moreover, these contagion effects were specific to the stimulus-motion properties of the observed stimuli. This shows that involuntary movement deviation in the axis orthogonal to the executed arm movement is not simply a consequence of observing a moving stimulus featuring incongruent end-points (Gowen et al., 2008; Stanley et al., 2007). Why, then, did observing the curvilinear stimulus result in the greatest orthogonal movement deviation? In answering this question, it is important to consider that the coding of trajectory information may be influenced by the presence of congruent or incongruent action features. That is, when the observed stimulus properties are closely matched (i.e., curvilinear), but not identical (i.e., horizontal) or opposite (i.e., vertical) to the concurrent executed movement, there is an increase in motor contagion (see Hommel et al., 2001).

Consistent with the theory of event coding, in which an action representation (observed or executed) comprises a series of codes reflecting individual action features (e.g., end-points, duration, trajectory, muscle groups) (Hommel et al., 2001), the greatest contagion is exhibited when there is co-activation of a single action feature (e.g., horizontal end-points) represented across multiple action representations (e.g., executed action and observed curvilinear stimulus). Conversely, less contagion will be exhibited when there is co-activation of action representations that share fewer action features (e.g., executed horizontal end-points versus observed vertical end-points). Put simply, the greater the congruence between observed and executed action features, then the greater motor contagion when presented with an incongruent trajectory.

Experiment 2

Introduction

The findings from the first experiment of increased contagion in the curvilinear compared to vertical condition occurred with the observed and executed actions parallel to each other. In this orientation, participants could move their arm when observing the curvilinear stimulus such that the maximum shoulder flexion and extension coincided with the spatial end-points of the observed stimulus. Accordingly, a shared action feature between the executed horizontal action and observed curvilinear stimulus leading to increased contagion could have resulted from the representation of external spatial coordinates (i.e., left and right of centre) and/or movements adopted at the end-points (i.e., horizontal flexion-extension).

To further examine the action features that influence motor contagion, a second experiment was conducted in which participants were instructed to perform horizontal arm movements in time with the vertical or curvilinear movement stimulus, but now facing either parallel or perpendicular to the stimulus display. In the perpendicular orientation, the end-points of the executed action were spatially incongruent to those of both the curvilinear and vertical stimuli. However, the executed action (i.e., horizontal arm movements) required the same agonist and antagonist muscle groups as those recruited in the parallel orientation. In this way, the end-points of the executed action when observing the curvilinear stimulus could be achieved using the same movement (horizontal shoulder flexion and extension) in the parallel and perpendicular torso orientation. However, for the vertical stimulus, the horizontal movement adopted at the end-points was incongruent irrespective of torso orientation.

A similar procedure in work on automatic imitation indicated priming of upper limb movements to anatomically congruent movement stimuli (e.g., executed index finger response coinciding with observed index finger movement) within a spatially incongruent perpendicular orientation (Heyes, Bird, Johnson, & Haggard, 2005; Press, Bird, Walsh, & Heyes, 2008). These results were taken as evidence of coding lower-level stimulus information related to the observed movement itself, as opposed to the spatial coordinates in which the stimulus moves. Therefore, it is predicted that if the observed end-points are represented within the underpinning movement dynamics then the increased deviation in the curvilinear condition should take place in both parallel and perpendicular orientations. Alternatively, if the end-points are represented in external spatial coordinates then the increased deviation in the curvilinear condition should be specific to the spatially compatible parallel orientation.

Method

Participants

Data was recorded from a different group of sixteen participants (aged between 18 to 21 years). All had normal or corrected-to-normal vision and gave written informed consent prior to taking part. The experiment was designed in accordance with the Declaration of Helsinki and was approved by the local ethics committee of the host university.

Task and Procedure

The task and practice procedures were essentially the same as in Experiment 1, except that participants performed horizontal arm movements while facing parallel or perpendicular to a display showing a vertical or curvilinear stimulus. Participants looked straight ahead for the parallel orientation and with the head turned toward the right shoulder for the perpendicular orientation (Fig. 5). The movement stimuli were randomly ordered with the caveat that no condition could be repeated consecutively, and the control trials were presented as the first and last trials. The stimulus conditions in the parallel and perpendicular orientations were presented in separate blocks, with the order counter-balanced across participants.

Insert Fig. 5 about here

Data collection and analysis

The data collection procedures and dependent measures were identical to Experiment 1. A 2 trial (first, last) x 2 orientation (parallel, perpendicular) mixed-design ANOVA was conducted on average deviation data in the control condition. To determine the effect of stimulus and orientation, the average deviation and peak position data were submitted to separate 2 stimulus (vertical, curvilinear) x 2 orientation (parallel, perpendicular) mixed-design ANOVA. Significant effects were decomposed using Bonferroni post hoc procedure ($p < 0.05$).

Results and Discussion

For control trials, there was a no significant main effect of trial, $F(1, 11) = 1.94$, $p > .05$, partial $\eta^2 = .15$, indicating no significant attentional or muscular fatigue effects. Although there was a significant main effect of orientation, $F(1, 11) = 15.89$, $p < .01$, partial $\eta^2 = .59$, there was no significant trial x orientation interaction, $F(1, 11) = 1.02$, $p > .05$, partial $\eta^2 = .08$.

For the analysis of movement deviation, there was a significant main effect of stimulus, $F(1, 15) = 12.66$, $p < .01$, partial $\eta^2 = .46$ (Fig. 6). As per Experiment 1, there was increased movement deviation in the curvilinear condition compared to the vertical condition. There was a significant main effect of orientation, $F(1, 15) = 6.73$, $p < .05$, partial $\eta^2 = .31$, indicating increased movement deviation in the perpendicular compared to parallel orientation. There was no significant stimulus x orientation interaction, $F(1, 15) = .15$, $p > .05$, partial $\eta^2 = .01$. Thus the effect of stimulus was independent of any influence of orientation.

Insert Fig. 6 about here

For the analysis of peak position, ANOVA revealed a significant main effect of stimulus, $F(1, 15) = 22.54$, $p < .01$, partial $\eta^2 = .60$ (Fig. 7). Peak position was significantly higher in the curvilinear compared to vertical condition. The main effect of orientation approached conventional levels of significance, $F(1, 15) = 3.41$, $p = .09$, partial $\eta^2 = .18$, indicating a higher peak position in the parallel compared to perpendicular orientation. There was no significant stimulus x orientation interaction, $F(1, 15) = .26$, $p > .05$, partial $\eta^2 = .08$.

Insert Fig. 7 about here

Consistent with the findings of Experiment 1, there was increased motor contagion in the curvilinear compared to vertical condition when facing parallel to the stimulus display. Also, while there were differences between the parallel and perpendicular orientations, these were independent of the stimulus effects. In other words, participants exhibited greater deviation in the perpendicular than parallel condition, which was simply added to the contagion resulting from the observed stimuli. A similar pattern of results was indicated in peak position data, thus adding further support to the suggestion that contagion was a result of coding the stimulus-motion properties within the observed stimulus. Although we cannot be certain, we suspect that the increase in movement deviation for the perpendicular orientation was related to the limited visual feedback of the arm (Khan, Franks, & Goodman, 1998). In combination, the findings from this experiment indicate that increased motor contagion in the curvilinear condition is not dependent on congruency between the external spatial coordinates of end-points with the stimulus and executed action.

General discussion

Previous studies have shown an increase in involuntary orthogonal arm movement deviation during the concurrent observation of incongruent human arm movements (Kilner et al., 2003; Kilner et al., 2007), which has been attributed to the trajectory and/or end-points within the observed movement stimuli (Gowen et al., 2008; Stanley et al., 2007). Here, we examined more directly the contribution of these action features on movement deviation during an interpersonal observation-execution task.

In the first experiment, we found motor contagion, as evidenced by average deviation in the orthogonal axis, was greater when observing a vertical compared to horizontal stimulus. There was even greater motor contagion in the curvilinear condition, which featured congruent end-points but incongruent trajectory. In accord with the theory of event coding (Hommel et al. 2001), we interpret these findings as evidence that motor contagion occurs through co-activation of action representations (observed stimulus or executed action) consisting of shared action features. A similar explanation was given for data showing that partially incongruent action stimuli increased contagion (as indicated by slowed response times) compared to identical and opposing action stimuli (Ocampo, Painter, & Kritikos, 2012). In the current study, the representations for the observed curvilinear stimulus and executed horizontal movement were incongruent in terms of trajectory, but shared common action features related to end-points.

In the second experiment we showed that end-points of the observed stimulus do not have to be located in the same orientation as the executed action (for similar effects on automatic imitation, see Heyes et al. 2005). Therefore, it would seem that this action feature (i.e., horizontal end-points) contributes to motor contagion because it is represented across multiple lower-level representations (executed action and observed stimulus), and not an abstract representation of the external spatial coordinates. This is consistent with the idea of motor contagion being underpinned by a bi-directional perceptual-motor process involving the co-activation of a particular action feature within incongruent action representations (Blakemore & Frith, 2005).

An alternative interpretation for the finding of increased movement deviation in the curvilinear compared to vertical (and horizontal) condition is that it could be reflective of a random disturbance related to motion saliency (Jansson, Wilson, Williams, & Mon-Williams, 2007). However, we know of no reason why curvilinear motion should be more salient than vertical motion, which in turn would be more salient than horizontal motion. Indeed, we found evidence for the mapping of stimulus-motion properties, which would not be predicted by some random disturbance. Visuomotor mapping is consistent with previous evidence indicating imitation of the movement direction of observed upper-limb movements (Dijkerman & Smit, 2007; Hardwick & Edwards, 2011). Further, it is coherent with the acquisition of novel motor skills through action-observation, where the mapping of stimulus-motion properties specifically relate to movement direction (Hayes, Ashford, & Bennett, 2008; Mattar & Gribble, 2005).

Another difference between the curvilinear and vertical (and horizontal) conditions is that the former had somewhat greater resultant velocity. This was an unavoidable consequence of preserving primary (horizontal or vertical) movement amplitude and cycle duration. In this respect, it is relevant to note that similar levels of movement deviation in the orthogonal axis have been reported when the frequency of an incongruent stimulus movement was varied between 0.5, 0.71 and 1.25Hz (Richardson, Campbell, & Schmidt, 2009). Therefore, simply trying to match horizontal arm movements to a faster moving incongruent stimulus should not influence orthogonal movement deviation. In the current study, however, there was incongruence between arm movement velocity in the primary horizontal axis and resultant velocity of the curvilinear stimulus. It will be interesting in future work to determine more precisely, albeit with biologically plausible stimuli, the incongruent factors between an executed action and observed trajectory that contribute to increased orthogonal deviation.

In summary, observing a curvilinear movement stimulus, featuring an incongruent trajectory, but end-points congruent with the executed horizontal arm movements, resulted in increased motor contagion compared to congruent horizontal or incongruent vertical stimuli.

Trajectory and end-points

Increased motor contagion when observing the curvilinear stimulus was found in both a spatially congruent (parallel) and incongruent (perpendicular) orientation. These contagion effects were reflected by the mapping of stimulus-motion properties related to the precise direction of the movement stimuli. Together, these findings support the theory of event coding (Hommel et al., 2001), which posits that the extent of motor contagion is determined by the stimulus action features shared with the executed action (i.e., movement end-points).

Footnote

1. In this instance, congruency of trajectory was defined by movement differences in the vertical axis. The additional movement in the vertical axis for the curvilinear stimulus was clearly different from the horizontal stimulus, and thus was conceived as an incongruent trajectory.

References

Blakemore, S. J. & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia, 43,* 260-267. doi: 10.1016/j.neuropsychologia.2004.11.012

Boria, S., Fabbri-Destro, M., Cattaneo, L., Sparaci, L., Sinigaglia, C., Santelli, E. … Rizzolatti, G. (2009). Intention understanding in autism. *PLoS ONE, 4,* e5596. doi: 10.1371/journal.pone.0005596

Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial and imitative cues. *Brain and Cognition, 44,* 124-143. doi: 10.1006/brcg.2000.1225

Cattaneo, L., Sandrini, M., & Schwarzbach, J. (2010). State-dependent TMS reveals a hierarchical representation of observed acts in the temporal, parietal, and premotor cortices. *Cerebral Cortex, 20,* 2252-2258. doi: 10.1093/cercor/bhp291

Chartrand, T. L. & Bargh, J. A. (1999). The chameleon effects: The perception-behavior link and social interaction. *Journal of Personality and Social Psychology, 76,* 893-910. doi: 10.1037//0022-3514.76.6.893

Csibra, G. (2007). Action mirroring and action understanding: An alternative account. In P. Haggard, Y. Rossetti, & M. Kawato (Eds.), *Sensorimotor foundations of higher cognition, attention and performance XXII* (pp. 435-459). Oxford: Oxford University Press.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research, 91,* 176-180. Retrieved from http://link.springer.com/journal/221/91/1/page/1

Dijkerman, H. C. & Smit, M. C. (2007). Interference of grasping observation during prehension, a behavioural study. *Experimental Brain Research, 176,* 387-396. doi: 10.1007/s00221-006-0627-z

Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *Neuroreport, 12,* 1489-1492. doi: 10.1097/00001756-200105250-00038

Gowen, E., Stanley, J., & Miall, R. C. (2008). Movement interference in autism-spectrum disorder. *Neuropsychologia, 46,* 1060-1068. doi: 10.1016/j.neuropsychologia.2007.11.004

Grafton, S. T. & Hamilton, A. F. (2007). Evidence of a distributed hierarchy of action representation in the brain. *Human Movement Science, 26,* 590-616. doi: 10.1016/j.humov.2007.05.009

Hamilton, A. F. D. & Grafton, S. (2006). Goal representation in human anterior intraparietal sulcus. *The Journal of Neuroscience, 26,* 1133-1137. doi: 10.1523/JNEUROSCI.4551-05.2006

Hardwick, R. M. & Edwards, M.G. (2011). Observed reach trajectory influences executed reach kinematics in prehension. *Quarterly Journal of Experimental Psychology, 64,* 1082-1093. doi: 10.1080/17470218.2010.538068

Hardwick, R. M. & Edwards, M. G. (2012). Motor interference and facilitation arising from observed movement kinematics. *Quarterly Journal of Experimental Psychology, 65,* 840-847. doi: 10.1080/17470218.2012.672995

Hayes, S. J., Ashford, D., & Bennett, S. J. (2008). Goal-directed imitation: The means to an end. *Acta Psychologica, 131,* 202-208. doi: 10.1016/j.actpsy.2009.05.002

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Cognitive Brain Research, 22,* 233-240. doi: 10.1016/j.cogbrainres2004.09.009

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences, 24,* 849-878. doi: 10.1017/S0140525X01000103

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science, 286,* 2526-2568. doi: 10.1126/science.286.5449.2526

Jansson, E., Wilson, A. D., Williams, J. H. G., & Mon-Williams, M. (2007). Methodological problems undermine tests of ideo-motor conjecture. *Experimental Brain Research, 182,* 549-558. doi: 10.1007/s00221-007-1013-1

Khan, M. A., Franks, I. M., & Goodman, D. (1998). The effect of practice on the control of rapid aiming movement: Evidence for an interdependency between programming and feedback processing. *The Quarterly Journal of Experimental Psychology, 51A,* 425-444. doi: 10.1080/713755756

Kilner, J. M., Hamilton, A. F., & Blakemore, S. J. (2007). Interference effect of observed human movement on action is due to velocity profile of biological motion. *Social Neuroscience, 2,* 158-166. doi: 10.1080/17470910701428190

Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology, 13,* 522-525. doi: 10.1080/17470910701428190

Mattar, A. A. G. & Gribble, P. L. (2005). Motor learning by observing. *Neuron, 46,* 153-160. doi: 10.1016/j.neuron.2005.02.009

Ocampo, B., Painter, D. R., & Kritikos, A. (2012). Event coding and motor priming: how attentional modulation may influence binding across action properties. *Experimental Brain Research, 219,* 139-150. doi: 10.1007/s00221-012-3073-0

Press, C. (2011). Action observation and robotic agents: learning and anthropomorphism. *Neuroscience and Biobehavioural Reviews, 35,* 1410-1418. doi: 10.1016/j.neubiorev.2011.03.004

Press, C., Bird, G., Walsh, E., & Heyes, C. (2008). Automatic imitation of intransitive actions. *Brain and Cognition, 67,* 44-50. doi: 10.1016/j.bandc.2007.11.001

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology, 9,* 129-154. doi: 10.1080/713752551

Richardson, M. J., Campbell, W. L., & Schmidt, R. C. (2009). Movement interference during action observation as emergent coordination. *Neuroscience Letters, 449,* 117-122. doi: 10.1016/j.neulet.2008.10.092

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience, 2,* 661-670. doi: 10.1038/35090060

Stanley, J., Gowen, E., & Miall, R. C. (2007). Effects of agency on movement interference during observation of a moving dot stimulus. *Journal of Experimental Psychology: Human Perception and Performance, 33,* 915-926. doi: 10.1037/0096-1523.33.4.915

Wohlschläger, A., Gattis, M., & Bekkering, H. (2003). Action generation and action perception in imitation: An instance of the ideomotor principle. *Philosophical*

Transactions of the Royal Society of London B, 358, 501-515. doi: 10.1098/rstb.2002.1257

Figure captions

Fig. 1 Pictorial representation of the horizontal (a), vertical (b) and curvilinear (c) stimuli. The dashed line in each panel indicates the direction of motion followed by the target dot. Movement traces of individual movement segments of the horizontal (d), vertical (e) and curvilinear (f) stimuli are included for comparison. Black and grey traces represent movement in the two segments that comprise a cycle

Fig. 2 Standard deviation within the orthogonal axis of movement during the observation of horizontal, vertical and curvilinear stimuli. Error bars show the within-group standard error

Fig. 3 Left (black) and right (grey) movement traces in the x- and y-axis taken from a single participant during the observation of horizontal (a), vertical (b) and curvilinear (c) stimuli

Fig. 4 Mean peak position within the orthogonal axis of movement during the observation of horizontal, vertical and curvilinear stimuli. Error bars show the within-group standard error

Fig. 5 Schematic representation of the parallel (a) and perpendicular (b) orientations. Thick black lines represent the projector screen; double-ended arrows represent the instructed horizontal movement direction, and dotted lines represent the equivalent viewing distance across orientation conditions

Fig. 6 Standard deviation within the orthogonal axis of movement during the observation of vertical and curvilinear stimuli in the parallel and perpendicular orientation. Error bars show the within-group standard error

Fig. 7 Mean peak position within the orthogonal axis of movement during the observation of vertical and curvilinear stimuli in the parallel and perpendicular orientation. Error bars show the within-group standard error