

LJMU Research Online

Roberts, JW, Hayes, SJ, Uji, M and Bennett, SJ

Motor contagion: the contribution of trajectory and end-points

https://researchonline.ljmu.ac.uk/id/eprint/1562/

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Roberts, JW, Hayes, SJ, Uji, M and Bennett, SJ (2015) Motor contagion: the contribution of trajectory and end-points. PSYCHOLOGICAL RESEARCH-PSYCHOLOGISCHE FORSCHUNG, 79 (4). pp. 621-629. ISSN 0340-0727

LJMU has developed LJMU Research Online for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact researchonline@ljmu.ac.uk

http://researchonline.ljmu.ac.uk/

1	Title: Motor contagion: the contribution of trajectory and end-points
2	
3	
4	Running head: Trajectory and end-points
5	
6	
7	
8	
9	James W. Roberts*, Spencer J. Hayes, Makoto Uji, Simon J. Bennett
10	
11	
12	
13	
14	Brain and Behaviour Laboratory,
15	Liverpool John Moores University, Liverpool, UK
16	
17	
18	
19	
20	*Corresponding author
21	Brain and Behaviour Laboratory, Faculty of Science, Liverpool John Moores University,
22	Byrom Street, Liverpool, L3 3AF, UK
23	Tel: +44 (0) 151 904 6237, Fax: +44 (0) 151 904 6284
24	J.W.Roberts@2006.ljmu.ac.uk
25	

1 Abstract

2 Increased involuntary arm movement deviation when observing an incongruent 3 human arm movement has been interpreted as a strong indicator of motor contagion. Here, 4 we examined the contribution of trajectory and end-point information on motor contagion by 5 altering congruence between the stimulus and arm movement. Participants performed cyclical 6 horizontal arm movements whilst simultaneously observing a stimulus representing human 7 arm movement. The stimuli comprised congruent horizontal movements or vertical 8 movements featuring incongruent trajectory and end-points. A novel, third, stimulus 9 comprised curvilinear movements featuring congruent end-points, but an incongruent 10 trajectory. In Experiment 1, our dependent variables indicated increased motor contagion 11 when observing the vertical compared to horizontal movement stimulus. There was even 12 greater motor contagion in the curvilinear stimulus condition indicating an additive effect of 13 an incongruent trajectory comprising congruent end-points. In Experiment 2, this additive 14 effect was also present when facing perpendicular to the display, and thus with end-points 15 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 16 17 that increased motor contagion takes place when observed and executed actions share 18 common features (i.e., movement end-points).

19

20 Keywords

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

1 Introduction

2 It is well accepted that there is a close link between perception and action, and 3 accordingly this has been recognised in numerous conjectures on the processes involved in 4 action-observation: common-coding (Prinz, 1997), theory of event coding (Hommel, Müsseler, Aschersleben, & Prinz, 2001) and direct-matching (Rizzolatti, Fogassi, & Gallese, 5 6 2001). Indeed, the discovery of so-called mirror neurons within the premotor cortex of the 7 monkey, which are activated during the observation and execution of a reach-and-grasp 8 action, provides neurobiological evidence to substantiate the commonality between 9 perception and action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). A similar 10 mirror system was subsequently identified within the fronto-parietal regions of the human 11 brain (Cattaneo, Sandrini, & Schwarzbach, 2010; Hamilton & Grafton, 2006; Iacoboni et al., 12 1999), and was postulated to have several behavioural consequences for action understanding 13 and social imitation (Boria et al., 2009; Chartrand & Bargh, 1999). For instance, automatic 14 imitation predicts that faster response times are made when a stimulus onset cue corresponds 15 with the pre-requisite movement response (e.g., a background image of an index finger 16 movement accompanying an index finger movement response; Brass, Bekkering, 17 Wohlschläger, & Prinz, 2000). In a similar vein, individuals performing an interpersonal 18 observation-execution task exhibit involuntary orthogonal arm movement deviation during 19 the observation of incongruent, as opposed to congruent, human arm movements (Kilner, 20 Paulignan, & Blakemore, 2003). The latter effect has been referred to as *motor contagion* 21 (Blakemore & Frith, 2005), and is thought to occur when the observed human stimulus 22 activates an internal representation that interferes with the efferent motor commands 23 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)

1 properties underpinning motor contagion. For example, Hardwick and Edwards (2012) 2 suggested that contagion results from incongruent spatial direction (lateral vs. anterior) when 3 performing an incongruent goal-directed action (horizontal flexion-extension of the shoulder 4 vs. flexion-extension of the elbow). Similarly, it has been suggested that arm movement 5 deviation associated with incongruent stimuli may be influenced by the incongruent end-6 points, as opposed to the trajectory (Gowen, Stanley, & Miall, 2008; Stanley et al., 2007). 7 The implication is that motor contagion, like several other behavioural effects during action-8 observation, may be mediated by a mirror system comprising multiple levels of action-9 representation (Csibra, 2007; Grafton & Hamilton, 2007; Wohlschläger, Gattis, & Bekkering, 10 2003).

11 While not intending to debate the findings of previous empirical or theoretical work 12 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 13 respect, it is notable that although Stanley et al. (2007) reported that motor contagion may be 14 15 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, 16 irrespective of the congruency of movement direction. The authors suggested this was a result 17 18 of the inherent variability in the observed biological motion, and thus a source of bottom-up 19 interference related to the trajectory. Thus, our aim was to examine the contribution of 20 trajectory and end-point information on motor contagion. Specifically, we aimed to determine 21 the effect of congruence between the executed action and the trajectory and/or end-point 22 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 23 24 stimuli as a non-human agent with biological motion properties.

1

Experiment 1

2 Introduction

3 Using a similar experimental design to that of Stanley et al. (2007), here we required 4 participants to perform cyclical horizontal arm movements across the mid-line of their body 5 whilst observing a moving dot stimulus representing pre-recorded human arm movement. 6 Two of the conditions of observed stimuli included horizontal movements similar to that 7 performed by the participant, or vertical movements featuring incongruent trajectory and end-8 points. An additional stimulus was generated that displayed a curvilinear trajectory, and thus 9 featured movement end-points congruent with the executed action, but an incongruent trajectory.¹ 10

11 It was hypothesised that if observed stimuli are primarily coded as a function of their 12 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 13 14 a result of incongruence between the executed action and observed trajectory, it can be 15 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 16 influence motor contagion (Hommel et al., 2001), it follows that movement deviation 17 18 exhibited in the curvilinear condition will differ from that of the vertical stimulus condition. 19 More specifically, if the coding of the observed incongruent action features elicits increased 20 motor contagion due to similarities with the executed action features then we would 21 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.

7

8 Method

9 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.

14

15 Stimuli

16 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 17 18 Precision 670) using the COGENT toolbox implemented in MATLAB (Mathworks Inc), and 19 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 20 21 data from the moving arm of a volunteer. The movements were well practised in order that 22 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 23 24 corresponded to either 400 mm horizontal or vertical displacement on the projection screen. 25 The movement stimuli consisted of cyclical horizontal and vertical arm movements. In

1	addition, participants were shown a cyclical curvilinear moving stimulus that displaced 400
2	mm in the horizontal axis and 200 mm in the vertical axis (from centre to the upper vertex).
3	Thus, the curvilinear movement end-points aligned with those of the horizontal stimulus (see
4	Fig. 1). Finally, we included a control condition in which a single red dot was presented at
5	screen centre for the duration of the trial. Participants were instructed to fixate on the
6	stationary stimulus while moving their arm at 400 mm horizontal amplitude. No instructions
7	were given to participants regarding the animacy of the moving stimulus.
8	

9

Insert Fig. 1 about here

10

11 Task and Procedure

12 Participants were instructed to perform 400 mm amplitude horizontal arm movements 13 across the mid-line of their body in time with a cyclical moving stimulus (or fixating on a 14 stationary stimulus) observed on the projection screen. The room was otherwise dark and 15 participants did not have any external cues regarding the location of the stimulus relative to 16 the screen edge and thus movement reversal. Initially, each participant performed two 17 practice trials with the guidance of stationary targets located 400 mm apart in the horizontal 18 axis and an auditory metronome. Participants were instructed to time their movement so that 19 the end-points, and thus reversals, coincided with the tones. Following practice, the stationary 20 targets and auditory metronome were removed, and participants completed a trial in the 21 control condition. Next they completed two trials in each of moving stimulus conditions, 22 which were randomly ordered with the caveat that no condition could be repeated 23 consecutively. Finally, they completed a second trial in the control condition. The control 24 condition was presented as the first and last trials in order to determine if there were 25 attentional and fatigue effects.

1

2 Data collection and analysis

3 The position of an active infrared sensor attached to the tip of the index finger was 4 recorded at 200 Hz using a 3D Investigator Motion Capture System (Northern Digital Inc., 5 Ontario, Canada). Following data acquisition, the first and last 5 s of data recording were 6 discarded in order to minimize asynchrony around movement onset and potential attentional and fatigue effects (Hardwick & Edwards, 2012). The remaining position data were then 7 8 filtered at 10 Hz using an autoregressive filter implemented in MATLAB. The same routine 9 next determined individual movement segments by identifying reversals in fingertip position 10 of the dominant movement axis (i.e., x-axis; horizontal). For each movement segment (i.e., a 11 half cycle) the standard deviation of fingertip position within the orthogonal movement axis 12 (i.e., y-axis; vertical) was calculated to provide a measure of motor contagion. The average 13 deviation across movement segments within a trial was calculated for each participant. In 14 addition, the mean peak position within the orthogonal axis was calculated to provide a 15 measure of mapping the stimulus-motion properties. Peak position was determined as the 16 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. 17

18 If there were mapping of the stimulus-motion properties to the participant's 19 movement, it can be expected that movement deviation would occur primarily in the upward 20 direction with the curvilinear stimulus (Fig. 1f), thus leading to a high mean peak position. 21 Looking at the vertical stimulus (Fig. 1e), it can be seen that there is deviation away from the 22 horizontal axis in the upward direction in one segment (positive) and downward direction in 23 the following segment (negative). Involuntary mapping of this motion by the participants 24 would lead to a lower mean peak position due to combining positive and negative deviation 25 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).

9

10 **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 =13 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.

15 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 16 movement deviation in the horizontal compared to the vertical (p < .05) and curvilinear (p < .05)17 18 .001) conditions. In addition, average deviation was significantly greater in the curvilinear 19 condition compared to the vertical condition (p < .05). The source of these effects can be 20 visualised in Fig. 3, which shows more vertical displacement over movement segments for 21 the vertical condition (Fig. 3b) compared to the horizontal condition (Fig. 3a), and yet even 22 greater displacement for the curvilinear condition (Fig. 3c). Indeed, the participants' 23 movement profile in the curvilinear condition was comparable to the observed curvilinear 24 stimulus (Fig. 1f).

Insert Fig. 2 and 3 about here

2	
3	For the analysis of peak position, ANOVA revealed a significant main effect of
4	stimulus, $F(2, 32) = 12.15$, $p < .001$, partial $\eta^2 = .43$ (Fig. 4). Post hoc comparisons indicated
5	a significant lower peak position in the horizontal condition compared to the vertical $(p > .01)$
6	and curvilinear conditions ($p > .01$). In addition, peak position in the curvilinear condition
7	was significantly higher than in the vertical condition ($p < .05$). As can be seen in Fig. 3c,
8	peak position in curvilinear condition was reflective of the primary upward movement for
9	both left (black trace) and right (grey trace) movement directions of the curvilinear stimulus.
10	However, when observing the vertical stimulus, participants moved mainly upwards in one
11	segment (black trace) and downwards (grey trace) in the following segment, thus leading to
12	peak position closer to zero.
13	
14	Insert Fig. 4 about here
15	
16	Consistent with previous work (Kilner et al., 2003; 2007), we found evidence of
17	motor contagion during the observation of a vertically-moving stimulus, and thus incongruent
18	trajectory and end-points. There was even greater motor contagion when participants
19	observed the curvilinear stimulus. Moreover, these contagion effects were specific to the
20	stimulus-motion properties of the observed stimuli. This shows that involuntary movement
21	deviation in the axis orthogonal to the executed arm movement is not simply a consequence
22	of observing a moving stimulus featuring incongruent end-points (Gowen et al., 2008;
23	Stanley et al., 2007). Why, then, did observing the curvilinear stimulus result in the greatest
24	orthogonal movement deviation? In answering this question, it is important to consider that
25	the coding of trajectory information may be influenced by the presence of congruent or

1 incongruent action features. That is, when the observed stimulus properties are closely

2 matched (i.e., curvilinear), but not identical (i.e., horizontal) or opposite (i.e., vertical) to the

3 concurrent executed movement, there is an increase in motor contagion (see Hommel et al.,

4 2001).

5 Consistent with the theory of event coding, in which an action representation 6 (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 7 8 is exhibited when there is co-activation of a single action feature (e.g., horizontal end-points) 9 represented across multiple action representations (e.g., executed action and observed 10 curvilinear stimulus). Conversely, less contagion will be exhibited when there is co-activation 11 of action representations that share fewer action features (e.g., executed horizontal end-points 12 versus observed vertical end-points). Put simply, the greater the congruence between 13 observed and executed action features, then the greater motor contagion when presented with 14 an incongruent trajectory.

- 15
- 16

Experiment 2

17 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).

3 To further examine the action features that influence motor contagion, a second 4 experiment was conducted in which participants were instructed to perform horizontal arm 5 movements in time with the vertical or curvilinear movement stimulus, but now facing either 6 parallel or perpendicular to the stimulus display. In the perpendicular orientation, the endpoints of the executed action were spatially incongruent to those of both the curvilinear and 7 8 vertical stimuli. However, the executed action (i.e., horizontal arm movements) required the 9 same agonist and antagonist muscle groups as those recruited in the parallel orientation. In 10 this way, the end-points of the executed action when observing the curvilinear stimulus could 11 be achieved using the same movement (horizontal shoulder flexion and extension) in the 12 parallel and perpendicular torso orientation. However, for the vertical stimulus, the horizontal movement adopted at the end-points was incongruent irrespective of torso orientation. 13

14 A similar procedure in work on automatic imitation indicated priming of upper limb 15 movements to anatomically congruent movement stimuli (e.g., executed index finger 16 response coinciding with observed index finger movement) within a spatially incongruent perpendicular orientation (Heyes, Bird, Johnson, & Haggard, 2005; Press, Bird, Walsh, & 17 Heyes, 2008). These results were taken as evidence of coding lower-level stimulus 18 19 information related to the observed movement itself, as opposed to the spatial coordinates in 20 which the stimulus moves. Therefore, it is predicted that if the observed end-points are 21 represented within the underpinning movement dynamics then the increased deviation in the 22 curvilinear condition should take place in both parallel and perpendicular orientations. 23 Alternatively, if the end-points are represented in external spatial coordinates then the 24 increased deviation in the curvilinear condition should be specific to the spatially compatible 25 parallel orientation.

1

2 Method

3 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.

8

9 Task and Procedure

10 The task and practice procedures were essentially the same as in Experiment 1, except 11 that participants performed horizontal arm movements while facing parallel or perpendicular 12 to a display showing a vertical or curvilinear stimulus. Participants looked straight ahead for 13 the parallel orientation and with the head turned toward the right shoulder for the 14 perpendicular orientation (Fig. 5). The movement stimuli were randomly ordered with the 15 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 16 17 orientations were presented in separate blocks, with the order counter-balanced across 18 participants.

- 19
- 20

Insert Fig. 5 about here

- 21
- 22 Data collection and analysis

The data collection procedures and dependent measures were identical to Experiment
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

1 stimulus and orientation, the average deviation and peak position data were submitted to

2 separate 2 stimulus (vertical, curvilinear) x 2 orientation (parallel, perpendicular) mixed-

3 design ANOVA. Significant effects were decomposed using Bonferroni post hoc procedure

4 (p < 0.05).

5

6 Results and Discussion

For control trials, there was a no significant main effect of trial, F(1, 11) = 1.94, p > 0.05, 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 $\eta^2 = .08$.

- 12 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 13 14 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 $\eta^2 = .31$, 15 indicating increased movement deviation in the perpendicular compared to parallel 16 orientation. There was no significant stimulus x orientation interaction, F(1, 15) = .15, p >17 .05, partial $\eta^2 = .01$. Thus the effect of stimulus was independent of any influence of 18 19 orientation. 20 21 Insert Fig. 6 about here
- 22

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

1	approached conventional levels of significance, $F(1, 15) = 3.41$, $p = .09$, partial $\eta^2 = .18$,
2	indicating a higher peak position in the parallel compared to perpendicular orientation. There
3	was no significant stimulus x orientation interaction, $F(1, 15) = .26$, $p > .05$, partial $\eta^2 = .08$.
4	
5	Insert Fig. 7 about here
6	
7	Consistent with the findings of Experiment 1, there was increased motor contagion in
8	the curvilinear compared to vertical condition when facing parallel to the stimulus display.
9	Also, while there were differences between the parallel and perpendicular orientations, these
10	were independent of the stimulus effects. In other words, participants exhibited greater
11	deviation in the perpendicular than parallel condition, which was simply added to the
12	contagion resulting from the observed stimuli. A similar pattern of results was indicated in
13	peak position data, thus adding further support to the suggestion that contagion was a result
14	of coding the stimulus-motion properties within the observed stimulus. Although we cannot
15	be certain, we suspect that the increase in movement deviation for the perpendicular
16	orientation was related to the limited visual feedback of the arm (Khan, Franks, & Goodman,
17	1998). In combination, the findings from this experiment indicate that increased motor
18	contagion in the curvilinear condition is not dependent on congruency between the external
19	spatial coordinates of end-points with the stimulus and executed action.
20	
21	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

1 examined more directly the contribution of these action features on movement deviation

2 during an interpersonal observation-execution task.

3 In the first experiment, we found motor contagion, as evidenced by average deviation 4 in the orthogonal axis, was greater when observing a vertical compared to horizontal 5 stimulus. There was even greater motor contagion in the curvilinear condition, which featured 6 congruent end-points but incongruent trajectory. In accord with the theory of event coding 7 (Hommel et al. 2001), we interpret these findings as evidence that motor contagion occurs 8 through co-activation of action representations (observed stimulus or executed action) 9 consisting of shared action features. A similar explanation was given for data showing that 10 partially incongruent action stimuli increased contagion (as indicated by slowed response 11 times) compared to identical and opposing action stimuli (Ocampo, Painter, & Kritikos, 12 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 13 14 action features related to end-points.

15 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 16 automatic imitation, see Heyes et al. 2005). Therefore, it would seem that this action feature 17 18 (i.e., horizontal end-points) contributes to motor contagion because it is represented across 19 multiple lower-level representations (executed action and observed stimulus), and not an 20 abstract representation of the external spatial coordinates. This is consistent with the idea of 21 motor contagion being underpinned by a bi-directional perceptual-motor process involving 22 the co-activation of a particular action feature within incongruent action representations 23 (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

1 random disturbance related to motion saliency (Jansson, Wilson, Williams, & Mon-Williams, 2 2007). However, we know of no reason why curvilinear motion should be more salient than 3 vertical motion, which in turn would be more salient than horizontal motion. Indeed, we 4 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 5 6 indicating imitation of the movement direction of observed upper-limb movements 7 (Dijkerman & Smit, 2007; Hardwick & Edwards, 2011). Further, it is coherent with the 8 acquisition of novel motor skills through action-observation, where the mapping of stimulus-9 motion properties specifically relate to movement direction (Hayes, Ashford, & Bennett, 10 2008; Mattar & Gribble, 2005). 11 Another difference between the curvilinear and vertical (and horizontal) conditions is 12 that the former had somewhat greater resultant velocity. This was an unavoidable consequence of preserving primary (horizontal or vertical) movement amplitude and cycle 13 14 duration. In this respect, it is relevant to note that similar levels of movement deviation in the 15 orthogonal axis have been reported when the frequency of an incongruent stimulus movement 16 was varied between 0.5, 0.71 and 1.25Hz (Richardson, Campbell, & Schmidt, 2009). 17 Therefore, simply trying to match horizontal arm movements to a faster moving incongruent 18 stimulus should not influence orthogonal movement deviation. In the current study, however, 19 there was incongruence between arm movement velocity in the primary horizontal axis and 20 resultant velocity of the curvilinear stimulus. It will be interesting in future work to determine 21 more precisely, albeit with biologically plausible stimuli, the incongruent factors between an 22 executed action and observed trajectory that contribute to increased orthogonal deviation. 23 In summary, observing a curvilinear movement stimulus, featuring an incongruent 24 trajectory, but end-points congruent with the executed horizontal arm movements, resulted in 25 increased motor contagion compared to congruent horizontal or incongruent vertical stimuli.

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

 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