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Automatic imitation of intransitive actions

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Abstract

Previous research has indicated a potential discontinuity between monkey and human ventral premotor-parietal mirror systems, namely that monkey mirror systems process only transitive (object-directed) actions, whereas human mirror systems may also process intransitive (non-object-directed) actions. The present study investigated this discontinuity by seeking evidence of automatic imitation of intransitive actions—hand opening and closing—in humans using a simple reaction time (RT), stimulus–response compatibility paradigm. Left–right and up–down spatial compatibility were controlled by ensuring that stimuli were presented and responses executed in orthogonal planes, and automatic imitation was isolated from simple and complex orthogonal spatial compatibility by varying the anatomical identity of the stimulus hand and response hemispace, respectively. In all conditions, action compatible responding was faster than action incompatible responding, and no effects of spatial compatibility were observed. This experiment therefore provides evidence of automatic imitation of intransitive actions, and support for the hypothesis that human and monkey mirror systems differ with respect to the processing of intransitive actions.

Keywords: Imitation; Stimulus–response compatibility; Spatial compatibility; Mirror system; Action observation

1. Introduction

Mirror neurons in the monkey ventral premotor cortex and parietal lobe fire both when the monkey executes an action and when it observes an experimenter executing the same action (e.g. Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Various methodologies have suggested that an analogous or homologous 'mirror system' is present in humans. For example, in a functional magnetic resonance imaging (fMRI) study, Iacoboni et al. (1999) found that both observing and executing finger actions activated the left ventral premotor cortex and right superior parietal lobule. However, not all of the current evidence indicates equivalence between monkey and human mirror systems. In particular, whereas mirror neurons in the ventral premotor-parietal mirror system discharge only when the monkey is observing or executing transitive (object-directed) actions, such as grasping (Umilta et al., 2001), there is some evidence from neurophysiological and behavioral studies that, in humans, this system may be active during the observation of both transitive and intransitive (non-object-directed) actions (e.g. Brass, Bekkering, Wohlschläger, & Prinz, 2000; Buccino et al., 2001; Heyes, Bird, Johnson, & Haggard, 2005; Iacoboni et al., 1999; Iacoboni et al., 2001; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; Koski et al., 2002; cf. Jonas et al., 2007). Supporting the neurological validity of the distinction between transitive and intransitive actions, research on apraxia has shown that left inferior parietal lesions are associated with impairment in the imitation of transitive, but not intransitive, actions (e.g. Buxbaum, Kyle, Grossman, & Coslett, 2007; see also Mozaz et al., 2006; Salter, Roy, Black, Joshi, & Almeida, 2004).

However, the research which suggests that the human ventral premotor-parietal mirror system may respond to intransitive actions is inconclusive. Studies have indicated influences of action observation on activation in cortical areas involved in action execution (imaging), action execu-

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tion itself (behavioral), and motor evoked potentials (MEPs, transcranial magnetic stimulation, TMS). There are at least two possible sources of this influence. First, as assumed in previous research, the observed action may activate specifically matching or 'mirroring' motor representations. Second, the observed actions have left–right and up–down spatial properties, and observation of these spatial properties could activate response codes corresponding to these spatial properties (e.g. Simon, 1990). For example, in a TMS study, Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) required participants to observe the experimenter trace geometric shapes in the air with his hand. When observing these actions, the participants exhibited enhanced MEPs in muscles involved in hand and arm movements. The enhancement may have been generated through activation of the specific motor representations of the movements observed. Alternatively, the observed actions contain up–down and left–right spatial features, and observation of these features may activate motor representations for moving up, down, left or right. Even in a recent MEP study where the effects of spatial variables were explored, the influence of spatial variables on the muscle specific effect of action observation was never investigated (Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006).

Behavioral studies commonly use automatic imitation (priming of action execution by action observation) as an index of mirror system functioning in humans. One recent study of this kind successfully dissociated automatic imitation from spatial compatibility (Bertenthal, Longo, & Kosobud, 2006). Building on the work of Brass et al., (2000; Brass, Bekkering, & Prinz, 2001), Bertenthal et al. (2006) used a stimulus–response compatibility paradigm in which participants were required to respond by tapping a key with the index or the middle finger of their right hand in the presence of video stimuli presenting the index or middle finger of another person's hand tapping a surface. The results showed that, when participants were instructed to produce a response which was spatially compatible with a stimulus movement, and therefore the stimulus action types were technically task-irrelevant, action compatible movements (e.g. index finger responses in the presence of index finger stimuli) were executed faster than action incompatible movements (e.g. index finger responses in the presence of middle finger stimuli). Thus, Bertenthal et al. (2006) found that, in humans, observation of index and middle finger tapping movements primes execution of the same movements, and that this may properly be regarded as an example of automatic imitation, rather than of spatially compatible responding, because it does not depend solely on activation by the stimulus movements of left–right relative position spatial codes (Brass et al., 2000).

However, the study by Bertenthal et al. (2006) does not tell us whether the human mirror system is responsive to intransitive actions because it involved movements that were transitive rather than intransitive. In contrast, the present study sought to dissociate automatic imitation from spatial compatibility using a pair of intransitive actions: opening and closing hand actions, observed and executed in the absence of objects, and in a manner that would not lead them to be interpreted as pantomimes of transitive actions. As illustrated in Fig. 1, in the terminal posture of hand opening, the fingers were splayed apart and stretched away from the palm. The opening action was much more exaggerated than that required simply to release an object from the hand. Similarly, in the terminal posture of hand closing, the fingers rolled into the palm, creating a fist. The action involved more complete closure of the hand than would be effective in grasping any object. A pilot study confirmed that these stimuli were perceived as intransitive actions, rather than pantomimes of grasping and releasing objects. When 30 participants were asked to give a spontaneous description of the stimuli, only three

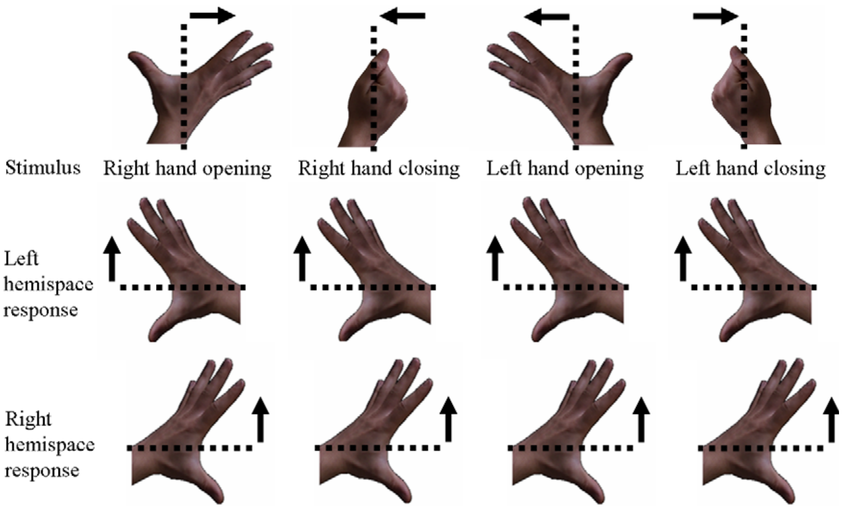

Fig. 1. Sample stimulus and response events, indicating for each event the principal axis of movement (dotted line), and the direction of finger movement (arrow). The top row shows all four stimuli used in the experiment (right hand opening, right hand closing, left hand opening, left hand closing). The middle row shows opening responses in left hemispace, and the bottom row shows opening responses in right hemispace.

used terms indicative of transitive actions (e.g. ‘grasping’, ‘holding’, ‘releasing’). In contrast, 27 participants used terms indicative of symbolic gestures (e.g. ‘closing’, ‘a fist’, ‘clenched’, ‘solidarity’, ‘revolution’, and ‘strong’ for the closing stimulus, and ‘opening’, ‘stretching’, ‘span’, ‘fly’, and ‘freedom’ for the opening stimulus).

In common with many previous studies of automatic imitation, we used a stimulus–response compatibility paradigm. In each block of our simple reaction time (RT) task, participants were instructed to perform a pre-specified response (e.g. to open their hand) as soon as they saw the stimulus hand begin to move. In half of the trials the stimulus hand opened and in half of the trials it closed. Automatic imitation was indexed by comparing RT on trials in which the stimulus movement was action compatible (e.g. opening stimulus and opening response), with trials in which stimulus movement was action incompatible (e.g. closing stimulus and opening response).

To control for left–right and up–down spatial compatibility, we presented hand stimuli in an up-right position, so that the fingers moved primarily in an horizontal plane (left–right), while requiring participants to respond with their hand prone, so that their fingers moved primarily in a vertical plane (up–down) (Heyes et al., 2005). With this arrangement, in which stimulus and response movements were made in orthogonal planes, stimulus and response movements that were action compatible (e.g. both opening) were not also left–right spatially compatible. However, this arrangement was not sufficient to control for spatial compatibility because a number of studies have reported orthogonal spatial compatibility effects in which up-right and down-left stimulus–response mappings are associated with faster responding than up-left and down-right mappings. For example, Weeks and Proctor (1990) found that participants were faster to execute key press responses to ‘X’ stimuli when right key responses were mapped to stimuli presented above (up) rather than below (down) fixation, and left key responses were mapped to stimuli presented below (down) rather than above (up) fixation. Further complicating the picture, up-right/down-left orthogonal spatial compatibility effects have been found only when responses are made in right hemispace or at body midline; when responses are made in left hemispace, the pattern is reversed with up-left/down-right mappings having the advantage (e.g. Cho & Proctor, 2004).

To control for orthogonal spatial compatibility, we varied the anatomical identity of the stimulus hand (left versus right), and response hemispace (left versus right) (Fig. 1). In the right hand stimulus, the fingers moved to the right during opening and to the left during closing, whereas in the left hand stimulus, they moved to the left during opening and to the right during closing. It has been found that orthogonal spatial compatibility effects which vary with response hemispace are not influenced by response hand (e.g. Cho & Proctor, 2004), and therefore our participants used their left hand to respond in right hemispace, and their right hand to respond in left hemispace.

Thus, in separate blocks of trials, participants responded (a) in left hemispace (with their right hand) to left hand stimuli, (b) in left hemispace to right hand stimuli, (c) in right hemispace (with their left hand) to left hand stimuli, and (d) in right hemispace to right hand stimuli. If performance in the present task is influenced by automatic imitation, then one would expect action compatible responding (e.g. opening response to an opening stimulus) to be faster than action incompatible responding (e.g. opening response to a closing stimulus) in each of these four conditions. If automatic imitation acts alone, that is, if orthogonal spatial compatibility has no influence on performance, then the magnitude of the action compatibility effect should not vary across conditions. If both automatic imitation *and* orthogonal spatial compatibility modulate responding then one would expect the action compatibility effect to be greater with the right stimulus hand than with the left stimulus hand, or, if orthogonal spatial compatibility varies by response hemispace, greater when responses in left hemispace are made to left rather than right hand stimuli, and when responses in right hemispace are made to right rather than left hand stimuli. Finally, if orthogonal spatial compatibility is the only influence on task performance, that is, if opening and closing intransitive actions are *not* automatically imitated, then one of two complex interactions should be observed. A global up-right/down-left advantage would give the impression that action compatible responding is faster than action incompatible responding to the right stimulus hand and slower than action incompatible responding to the left stimulus hand. Alternatively, if there is an up-right/down-left advantage for responses in right hemispace, and an up-left/down-right advantage for responses in left hemispace, then action compatible responding would appear to be faster than action incompatible responding when responses in left hemispace are made to left hand stimuli and responses in right hemispace are made to right hand stimuli, but slower than action incompatible responding when responses in left hemispace are made to right hand stimuli and responses in right hemispace are made to left hand stimuli.

2. Materials and methods

2.1. Participants

Sixteen consenting, healthy volunteers with an average age of 24.9 years, four male, took part in the experiment, and were paid a small honorarium for their participation. All were right-handed, had normal or corrected-to-normal vision, and were naïve with respect to the purpose of the experiment.

2.2. Stimuli

All stimuli were presented on a computer screen (60 Hz, 400 mm, 96DPI), in color on a black background, and viewing was unrestrained at a distance of approximately

600 mm. Each imperative stimulus was a right or a left hand, either opening or closing, filmed from the angle at which one normally views ones own hands (see Fig. 1). The left hand stimulus was created by flipping the right hand stimulus on the vertical axis. Both actions began with the fingers closed and pointing upwards in parallel with the thumb (warning stimulus). The warning stimulus subtended approximately 10.7° of visual angle horizontally and 16.4° vertically. The last frame of the opening action stimulus subtended approximately 20.2° of visual angle horizontally and 16.7° vertically, whereas the last frame of the closing action stimulus subtended approximately 10.6° horizontally and 15.1° vertically. Each action consisted of 12 frames and was of 480 ms duration.

2.3. Data recording and analysis

For both opening and closing responses, response onset was measured by recording the electromyogram (EMG) from the first dorsal interosseus muscle using disposable Ag/AgCl surface electrodes. Signals were amplified, mains-hum filtered at 50 Hz and digitised at 2.5 kHz. They were rectified and smoothed using a dual-pass Butterworth filter, with cut-off frequencies of 20 Hz and 1000 Hz. To define a baseline, EMG activity was registered for 100 ms when the participant was not moving at the beginning of each trial. A window of 20 ms was then shifted progressively over the raw data in 1 ms steps. Response onset was defined by the beginning of the first 20 ms window after the imperative stimulus in which the standard deviation for that window, and for the following 20 ms epoch, was greater than 2.75 times the standard deviation of the baseline. This criterion was chosen during initial calibration of the equipment as the most effective in discriminating false positives from misses. Whether the criterion correctly defined movement onset in the present experiment was verified by sight for every trial performed by each participant. Stimulus onset marked the beginning, and EMG onset marked the end, of the RT interval. Errors were recorded manually.

2.4. Procedure

Participants were tested individually in a dimly lit room. The participant's forearm lay in a horizontal position across his/her body, parallel with the stimulus monitor. It was supported from elbow to wrist by an armrest, and therefore the participant's hand was free to move. The wrist was rotated so that the fingers moved upwards during opening responses, and downwards during closing responses. Therefore, given that stimulus actions were presented in the lateral plane (left–right), response movement direction was orthogonal to stimulus movement direction. After making each response, participants were required to return their hand to the neutral starting position.

In each block of the simple RT task, participants were required to make the same pre-specified response in every trial. They were instructed to make this pre-specified response (to open or close their right or left hand) as quickly as possible after the stimulus hand began to move. There were four blocks in which closing was the required response and four in which opening was the required response. Participants completed all blocks with one response hand before completing the blocks with the other response hand. The order in which response hands were used (left first or right first) was counterbalanced, as was the order in which responses were executed (open first or close first). Participants were instructed to refrain from moving their hand in catch trials, when the stimulus hand did not move.

All trials began with presentation of the warning stimulus. In stimulus trials, this was replaced 800, 1600 or 2400 ms later by onset of the opening or closing stimulus, which was of 480 ms duration. After the imperative stimulus action, the screen went black for 3000 ms before the warning stimulus for the next trial appeared. In catch trials, the warning stimulus remained on the screen for 2880 ms before the 3000 ms inter-trial interval. Each block presented, in random order, 60 stimulus trials and 12 catch trials. There were five stimulus trials of each type, defined by factorial combination of the stimulus action (opening and closing), stimulus hand (left and right) and stimulus onset asynchrony (800, 1600, 2400 ms) variables.

Before testing commenced in each block, participants completed 12 practice trials (five opening stimulus, five closing stimulus and two catch trials) with the response to be used in that block.

3. Results

Participants initiated movement in 3.1% of catch trials. These data were not analyzed further. Practice trials, incorrect response types (0.07%) and response omissions (0.20%) were excluded from the analysis. There were no RTs smaller than 100 ms or greater than 1000 ms. On each trial, the pre-specified response was either action compatible with the stimulus (e.g. opening response to opening stimulus) or action incompatible with the stimulus (e.g. opening response to closing stimulus). The RT data, shown in Fig. 2, were subjected to ANOVA in which action compatibility (compatible and incompatible), stimulus hand (left or right) and response hemispace (left or right), were within-subject variables.

As shown in Fig. 2, an action compatibility effect was observed in all four conditions, suggesting that task performance was influenced by automatic imitation. On average, action compatible responses were 22 ms faster than action incompatible responses ($F(1, 15) = 10.7$, $p < .01$). There was no evidence that the magnitude of the action compatibility effect varied with the anatomical identity of the stimulus hand (action compatibility × stimulus hand, $F(1, 15) < 1$). This indicates that performance was not influenced by 'simple' orthogonal spatial compatibility; responding in trials involving up-right/down-left spatial

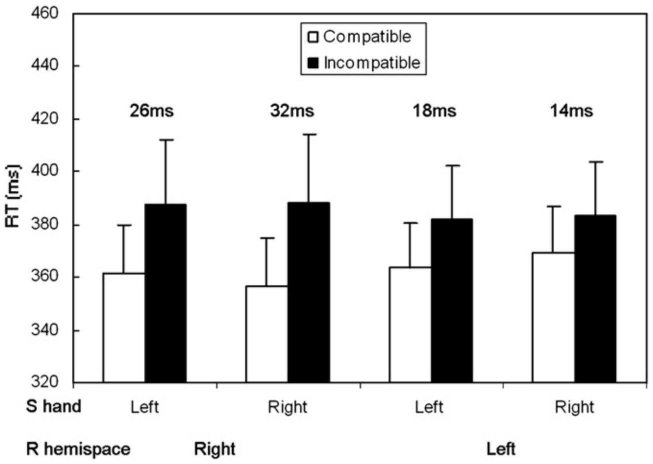

Fig. 2. Mean RT on action compatible (open bars) and incompatible (shaded bars) trials as a function of stimulus hand (left or right) and response hemispace (left or right). Vertical bars indicate the standard error of the mean. Numbers indicate the magnitude of the compatibility effect.

mappings was *not* generally faster than trials involving up-left/down-right mappings. Inspection of Fig. 2 suggests that the action compatibility effect was slightly larger when responses in left hemispace were made to left rather than right hand stimuli, and that responses in right hemispace were larger when made to right rather than left hand stimuli. This interaction was not significant ($F(1,15) = 2.1$, $p = .2$) but, owing to its theoretical significance, ANOVA was applied separately to the data from left and right hemispace responses. These analyses did not find a significant action compatibility × stimulus hand interaction for responses in left hemispace ($F(1,15) < 1$) or for responses in right hemispace ($F(1,15) = 3.0$, $p = .1$). Thus, there was no significant evidence of ‘complex’ orthogonal spatial compatibility, that is, of an up-right/down-left advantage for responses in right hemispace, or of an up-left/down-right advantage for responses in left hemispace.

4. Discussion

Previous research has indicated that, whereas the monkey ventral premotor-parietal mirror system is responsive only to transitive actions, the human mirror system may process both transitive and intransitive actions. To investigate this potential discontinuity, the present study sought evidence of automatic imitation of intransitive actions—hand opening and closing—in human participants, using a simple RT, stimulus–response compatibility paradigm. The experiment controlled for left–right and up–down spatial compatibility by ensuring that stimuli were presented and responses were executed in orthogonal planes, and isolated automatic imitation from ‘simple’ and ‘complex’ orthogonal spatial compatibility by varying the anatomical identity of the stimulus hand and response hemispace, respectively. The results showed that participants were faster to execute action compatible responses (e.g. opening responses to opening stimuli) than action incompatible responses (e.g. opening responses to closing stimuli) in all conditions. This pattern indicates that the intransitive actions were automatically imitated—and provides no evidence that performance was also influenced by orthogonal spatial compatibility.

This study therefore provides support for the hypothesis that human and monkey mirror systems differ with respect to their processing of intransitive actions. Broadly speaking, any differences between human and monkey mirror systems may be explained in two ways (Heyes, 2003). First, the difference may be primarily phylogenetic; for example, based on adaptive change in the hominid line driven by natural selection. Alternatively, the difference may be primarily ontogenetic; based on adaptive change occurring during the lifetime of individuals and driven by experience. The phylogenetic hypothesis is consistent with the widely held, but seldom stated, assumption that the mirror system, whether human or monkey, is a dedicated ‘module’, a product of very specific selection pressures (e.g. Gallese & Goldman, 1998). The alternative, ontogenetic hypothesis is consistent with a growing body of evidence showing that mirror system function can be modulated by experience, both in humans (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard 2005; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Haslinger et al., 2005; Heyes et al., 2005; Tessari & Rumiati, 2004; Vogt, Taylor, & Hopkins, 2003) and in monkeys (Ferrari, Rozzi, & Fogassi, 2005). The associative sequence learning (ASL) model (Brass & Heyes, 2005; Heyes, 2005; Heyes & Ray, 2000), and Keysers and Perrett’s Hebbian model (Keysers & Perrett, 2004), suggest that the mirror system develops through associative learning (see also Hommel, Müsseler, Aschersleben, & Prinz, 2001), and that the learning process is driven by experience in which specific actions—those to which the system will subsequently be responsive—are concurrently observed and executed. Experience of this kind is obtained by self-observation, socially synchronous action, and when the individual is being imitated by others. Therefore, these ontogenetic theories would suggest that, compared with the monkey mirror system, the human mirror system is more responsive to intransitive actions because these predominantly communicative behaviors are more common and more important in the human repertoire, and humans have more opportunity to observe and execute them concurrently. They would predict that, if monkeys were given appropriate training, their mirror systems would become responsive to intransitive actions. This hypothesis that the mirror systems of monkeys could, in principle, respond to intransitive actions is given some support by the finding that, in contrast to the usual behavior of monkeys, three monkeys studied by Kumashiro et al. (2003) showed some signs of imitation of intransitive actions.

In common with Brass et al. (2001) and Bertenthal et al. (2006), we have characterized our experiment as seeking to distinguish automatic imitation from spatial compatibility. This is useful shorthand, but it would be more accurate to say that, in their different ways, the studies have distinguished automatic imitation from *other types of* spatial compatibility. This characterization is more precise because it acknowledges that actions differ in terms of their configural spatial features, and therefore, at least at the descriptive level, automatic imitation is a species of spatial compatibility. For example, the difference between hand opening and hand closing consists in the way that the spatial relationships between hand parts (e.g. palm, fingers and finger segments) change over time. The observation that actions are processed in terms of configural spatial relations is consistent with the known properties of the superior temporal sulcus (STS), which is an area thought to provide the primary input to the ventral premotor-parietal mirror system (Iacoboni, 2005). For example, single-unit recording in monkeys suggests that the firing rate of many neurons in STS does not distinguish viewpoint (e.g. Jellema & Perrett, 2006), or left from right arm movement (Jellema, Baker, Wicker, & Perrett, 2000), but does distinguish configural spatial relations (e.g. rotation of the torso with respect to the lower body). Similarly, Thompson, Clarke, Stewart, and Puce (2005) found that the STS is equally active when humans observe up-right and inverted walking stimuli (cf. Grossman & Blake, 2001).

5. Conclusion

The results of the present study confirm those of previous studies in showing that automatic imitation is not merely a left–right or up–down spatial compatibility effect. They extend the findings of the previous studies by showing that automatic imitation is also distinct from orthogonal spatial compatibility, and, most importantly, by providing evidence that, in humans, intransitive actions are subject to automatic imitation.

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