Research Report

Robotic movement elicits automatic imitation

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Abstract

Recent behavioural and neuroimaging studies have found that observation of human movement, but not of robotic movement, gives rise to visuomotor priming. This implies that the 'mirror neuron' or 'action observation–execution matching' system in the premotor and parietal cortices is entirely unresponsive to robotic movement. The present study investigated this hypothesis using an 'automatic imitation' stimulus–response compatibility procedure. Participants were required to perform a prespecified movement (e.g. opening their hand) on presentation of a human or robotic hand in the terminal posture of a compatible movement (opened) or an incompatible movement (closed). Both the human and the robotic stimuli elicited automatic imitation; the prespecified action was initiated faster when it was cued by the compatible movement stimulus than when it was cued by the incompatible movement stimulus. However, even when the human and robotic stimuli were of comparable size, colour and brightness, the human hand had a stronger effect on performance. These results suggest that effector shape is sufficient to allow the action observation–matching system to distinguish human from robotic movement. They also indicate, as one would expect if this system develops through learning, that to varying degrees both human and robotic action can be 'simulated' by the premotor and parietal cortices.

1. Introduction

In humans and monkeys, observation of human action gives rise to matching motor activation; to activity in the premotor and parietal cortices normally associated with execution of the observed action. Visuomotor priming of this kind has been demonstrated using a variety of neurophysiological techniques, including single cell recording [14,34,40], functional magnetic resonance imaging (fMRI) [5,18,19,24], positron emission tomography (PET) [16,17], electroencephalography (EEG) [3,9,29] and transcranial magnetic stimulation (TMS) [2,30,35]. At the behavioural level, visuomotor priming takes the form of 'automatic

imitation' [23]; in the absence of instruction to imitate, movement observation facilitates execution of the observed movement and/or interferes with performance of an alternative movement. For example, research using stimulus–response compatibility (SRC) paradigms has shown that responses to human body movement stimuli (e.g. a video image of a hand opening) are faster and more accurate when they involve execution of the same movement (hand opening) than when they involve execution of an alternative movement (hand closing) and that this compatibility effect is present even when the identity of the stimulus movement (open or close) is task-irrelevant [4,12,23,36,41].

It has been suggested that visuomotor priming is part of a 'simulation' process which enables individuals to recognise the actions of others and thereby to apprehend their mental states [13,15,25]. For example, Kilner et al. [27, p.525], referring to Gallese [13], note: 'it has been proposed that the

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mirror system might have evolved to facilitate communication, empathy, and the understanding of other people's mental states. Simulating other people's actions would trigger an action representation from which the underlying goals and intentions could be inferred on the basis of what our own goals and intentions would be for the same action'. This hypothesis about the function of visuomotor priming is consistent with evidence that patients with Moebius syndrome, involving congenital paralysis of the facial muscles, are impaired in the recognition of facial expressions of emotion [10,11].

It is generally assumed that humans and some other animals have mental states, whereas machines do not. If this is correct, and if the function of visuomotor priming is to support inferences about mental states, visuomotor priming by mechanical movements could be maladaptive. It may result in false attribution of mental states to machines. Therefore, the simulation hypothesis is also consistent with recent reports that observation of the movements of mechanical devices, even when they are robotic (i.e. similar in appearance to human movements), does not give rise to visuomotor priming [7,14,27,28,39]. Single-cell recording has shown that 'mirror neurons' in area F5 of the monkey premotor cortex fire when the monkey grasps an object and when it observes a human hand grasping the same object, but not when the monkey sees the object grasped by a mechanical pincer [14]. Similarly, PET has detected significant activation in the left premotor cortex when human participants observed manual grasping actions performed by a human model, but not when they were performed by a robotic hand/arm [39].

The results of behavioural studies also indicate that robotic movements do not support visuomotor priming. In a task involving the separation of two parts of an object, Meltzoff [28] reported that 18-month-old infants completed the task after observing a demonstration by a human adult, but not after a demonstration performed by a mechanical device. In a series of experiments with healthy adults, Castiello et al. [7] found that components of manual grasping movements, such as maximum grip aperture and time to reach peak velocity, are affected by prior observation of a human model grasping an object of the same or different size and are not influenced by prior observation of a robotic hand/arm performing the same tasks. Similarly, Kilner et al. [27] showed that performance of sinusoidal arm movements in a vertical or horizontal plane was subject to interference from simultaneous observation of another human performing incompatible arm movements, i.e. movement in the opposite plane. However, when the model was a full-size robot – with head, trunk, arms and legs – rather than a human, execution of the prespecified movements was unimpaired by simultaneous observation of incompatible responding.

These findings imply that the system which mediates visuomotor priming – the 'mirror neuron' [33] or 'action observation–execution matching' [6] system – distin-

guishes categorically between biological movement of a human model and mechanical movement of a robot and that it is entirely unresponsive to the latter. On the assumption that robots do not have mental states or that the system evolved in a robot-free environment, lack of responsiveness to robotic movement is consistent with the hypothesis that the function of visuomotor priming is to support inferences about mental states [13,15,25]. However, there are both empirical and theoretical grounds for further more systematic investigation of the hypothesis that robotic movement does not support visuomotor priming.

The empirical evidence is inconclusive because the studies which have reported visuomotor priming for human but not for robotic stimuli have involved very little stimulus control. Typically, they have used just one token of the robotic stimulus type (one movement pattern performed by a single robot), and the appearance of this robotic movement token differed from that of the human movement tokens on a number of dimensions, e.g. shape, kinematics, size, colour and luminance. It is possible, therefore, that the robotic stimuli in these experiments failed to support visuomotor priming because they were insufficiently salient or, being less variable than the human movement stimuli, were more readily habituated. This would be implausible if all studies comparing visuomotor priming by human and robotic stimuli had similar results, but there is an exception. One study of object grasping found equivalent effects on movement duration, deceleration time and maximum grip aperture of observing a robotic hand and a human hand [[6], Experiment 1].

Recent theoretical work also suggests that further investigation of robotic movement stimuli is required. Analyses of behavioural data on imitation [20,22,23] and of the physiological properties of cortical areas involved in visuomotor priming [26] have converged on an associative learning hypothesis. This hypothesis suggests that the potential for visuomotor priming is learned through experience in which the individual contiguously observes and executes the same actions. For example, visuomotor priming of hand movements depends on cortical links established during visual observation of ones' own hand while performing such movements. Stimulus generalisation is a ubiquitous feature of associative learning [31]; the effects of training with a stimulus, X, are not only present in behaviour toward X, but also in behaviour elicited by other stimuli to the extent that those stimuli have physical characteristics in common with X. Therefore, if the associative learning hypothesis is correct, one would not expect robotic movement stimuli to be uniformly incapable of supporting visuomotor priming. Instead, one would expect robotic movements to support visuomotor priming to the extent that they resemble the human movements observed during acquisition of the cortical connections that mediate priming.

The present study investigated these predictions of the associative learning hypothesis by comparing the visuomo-

tor priming potential of human and robotic movement stimuli under more precisely controlled conditions than in previous studies. The procedure was based on an SRC task in which participants are required to make a prespecified hand movement (e.g. opening) on presentation of a compatible (opened) or incompatible (closed) movement stimulus. Previous experiments using this procedure with human movement stimuli have shown that responding is faster when the stimulus and response movements are compatible than when they are incompatible and that this automatic imitation effect is not due solely to spatial compatibility; it occurs even when the stimulus and responding hands move in orthogonal planes [23]. They have also indicated that the visual priming effect of terminal posture stimuli, such as those used in the present experiment, is at least as great as that of moving images of hand movement [36].

The stimulus hand in the present study was either human or robotic. There were two tokens or 'styles' of each of these stimulus types, one naturalistic and the other schematic. The human and robotic naturalistic stimuli differed in colour and luminance but were of a similar size and did not differ kinematically. Thus, although they were photographic images of a human hand and a robot hand, the naturalistic stimuli were better controlled than in most previous studies of visuomotor priming by robotic movement. The human and robotic schematic stimuli were even more precisely matched; they differed in shape but were of the same size, colour and luminance. For both naturalistic and schematic stimuli, kinematic variables were controlled by the use of terminal postures, rather than moving images, as action stimuli. If any difference between the visuomotor priming effects of human and robotic stimuli is present both when they are naturalistic and when they are schematic, it would suggest that the difference is due to shape cues that distinguish these two stimulus categories rather than to nonspecific attentional effects of variation in colour and brightness.

The results of previous studies suggest that the system mediating visuomotor priming is completely unresponsive to robotic movement stimuli. If this is correct, one would expect the human stimuli, but not the robotic stimuli, to elicit automatic imitation. That is, responding should be faster when human stimuli are response compatible than when they are response incompatible, but performance should not vary between compatible and incompatible trials with robotic stimuli.

The associative learning hypothesis predicts that the human stimuli will elicit a stronger automatic imitation effect than robotic stimuli because the human stimuli more closely resemble those encountered, through self-observation, during development of the system mediating visuomotor priming. However, this hypothesis also suggests that robotic stimuli will elicit automatic imitation to the extent that they resemble human movement stimuli. Compared with previous studies, the robotic stimuli in

the present experiment more closely resembled the comparison human stimuli in terms of size, colour and brightness. Therefore, the associative learning hypothesis predicts that, although the effect will be smaller than with human stimuli, the robotic stimuli will also elicit automatic imitation. Thus, both hypotheses predict an interaction between stimulus–response compatibility and stimulus type, but only the associative learning hypothesis predicts a reliable effect of compatibility when the stimuli are robotic.

2. Materials and methods

2.1. Participants

Sixteen consenting healthy participants with an average age of 25.4 years, six male, were recruited from within the Department of Psychology, University College London and paid a small honorarium for their participation. All were right-handed, had normal or correct-to-normal vision and were naive with respect to the purpose of the experiment. The experiment was performed with local ethical committee approval and in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.2. Stimuli

All stimuli were presented on a computer screen (60 Hz, 400 mm, 96 DPI) in colour on a black background. Viewing was unrestrained at a distance of approximately 600 mm. Each imperative stimulus was a naturalistic or a schematic representation of a human or a robotic hand in an opened or a closed posture. It was preceded by a warning stimulus representing a neutral posture of the same hand type (human or robotic) in the same style (naturalistic or schematic). The four stimulus formats (human naturalistic, robotic naturalistic, human schematic, robotic schematic) are shown in Fig. 1.

Details of the size (width and height), luminance and surface area of the stimuli are given in Table 1. The schematic human and robotic stimuli differed in shape but were controlled for colour (all were blue), size, luminance and surface area. The naturalistic human and robotic stimuli differed in shape, colour palette (flesh vs. metallic tones), luminance and surface area. The human stimuli were slightly brighter and occupied a larger area of the screen. Although not identical, the sizes of the naturalistic human and robotic stimuli were similar. The human hands appeared approximately life-size.

2.3. Data recording and analysis

For both open and close responses, response onset was measured by recording the electromyogram (EMG) from

A Human Naturalistic

B Robotic Naturalistic
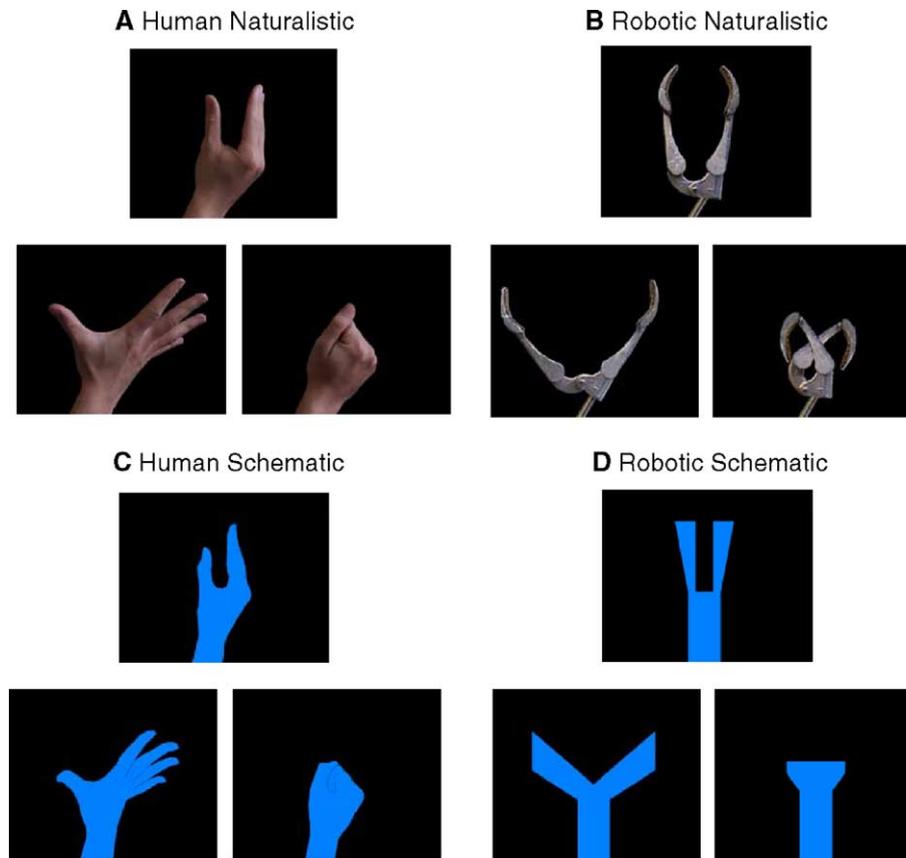
C Human Schematic

D Robotic Schematic

Fig. 1. Experimental stimuli: (A) human naturalistic, (B) robotic naturalistic, (C) human schematic, (D) robotic schematic. Within each panel, the top image is the warning stimulus, and the two images below are the opened (left) and closed (right) imperative stimuli.

the first dorsal interosseus (FDI) muscle using disposable Ag/AgCl surface electrodes. Signals were amplified, high-pass-filtered at 20 Hz, mains-hum-filtered at 50 Hz and digitised at 2.5 kHz. They were rectified and smoothed using a dual-pass Butterworth filter, with a cut-off frequency of 50 Hz. Signals were not low-pass-filtered. 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 response time (RT) interval. Errors were recorded manually.

Table 1
Visual angle, luminance and surface area values for each posture in each stimulus format

Stimulus type	Stimulus style	Posture	Width degrees of visual angle	Height degrees of visual angle	Relative luminance	Surface area cm^2
Human	Naturalistic	Opened	20.2	16.7	75	154
		Neutral	10.7	16.4	75	109
		Closed	10.6	13.6	68	94
Robotic	Naturalistic	Opened	20.2	16.5	93	67
		Neutral	10.4	18.5	96	67
		Closed	9.7	12.5	89	66
Human and robotic	Schematic	Opened	15.7	15.7	127	103
		Neutral	7.5	17.0	127	77
		Closed	7.5	12.0	127	68

Relative luminance was measured on a scale between 0 (completely black) and 255 (completely white).

2.4. Procedure

Participants were tested individually in a dimly lit room. The participant's right 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 when closing. Therefore, given that stimulus postures were presented in the lateral plane (left–right), response movements were orthogonal to stimulus postures. After making each response, participants were required to return their hand to a neutral starting position.

In each block of the simple RT task, participants were required to make a prespecified response (to open or to close their right hand) as soon as an imperative stimulus (an opened or closed posture) appeared on the screen. They were instructed to refrain from moving their hand in catch trials, when the imperative stimulus was not presented.

All trials began with presentation of the warning stimulus. In stimulus trials, this was replaced 800–1500 ms later by an imperative stimulus, which was of 480 ms duration. The stimulus onset asynchrony (SOA) varied randomly between 800 and 1500 ms in 50 ms steps. After the imperative stimulus, 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 1980 ms before the 3000 ms inter-trial interval. Each block presented, in random order, 15 trials in which the imperative stimulus was an opened posture, 15 trials in which the imperative stimulus was a closed posture, and 6 catch trials.

Human naturalistic, robotic naturalistic, human schematic and robotic schematic stimuli were presented in separate blocks. Participants completed four blocks with each of these four stimulus formats, two in which closing was the required response and two in which opening was the required response. Testing was conducted over 2 days, with one open response and one close response block of each stimulus type completed each day. Within each day, blocks requiring the same response were completed consecutively, and those involving the same stimulus type (human or robotic) were completed in immediate succession. For each participant, the order of stimulus formats (human naturalistic, robotic naturalistic, human schematic and robotic schematic) was the same for blocks in which they were making open and close responses and constant across the first and second days of testing. We counterbalanced the order in which responses were tested (open first or close first), and the order of blocks distinguished by stimulus type (human first or robotic first) and stimulus style (schematic first or naturalistic first).

Before testing commenced in each block, participants completed five practice trials (two open stimulus, two close stimulus and one catch trial) with the response, and to the stimuli, to be used in that block.

3. Results

Practice trials, incorrect responses (0.02%) and response omissions (0.04%) were excluded from the analysis, as were all RTs smaller than 100 ms and greater than 1000 ms (0.05%). On each trial, the stimulus posture was either the same as (compatible) or different from (incompatible) the prespecified response. The RT data, shown in Fig. 2, were subjected to analysis of variance (ANOVA) in which stimulus–response compatibility (compatible and incompatible), stimulus type (human and robotic) and stimulus style (naturalistic or schematic) were within-Ss variables.

This analysis revealed a significant main effect of compatibility, $F(1,15) = 21.4$, $P < 0.001$, and a significant stimulus type × compatibility interaction, $F(1,15) = 25.1$, $P < 0.001$. On average, responding was 18 ms faster on compatible trials ($M = 279.2$ ms, SEM = 13.7 ms) than on incompatible trials ($M = 297.5$ ms, SEM = 15.9 ms), and the compatibility effect was greater when participants were responding to human stimuli (27.9 ms) than when they were responding to robotic stimuli (8.8 ms) (see Fig. 2). Simple effects analysis indicated that the difference in RT between compatible and incompatible trials was significant, not only when the stimuli were human, $F(1,15) = 30.4$, $P < 0.0001$, but also when they were robotic, $F(1,15) = 5.9$, $P < 0.03$). No other effects or interactions were significant.
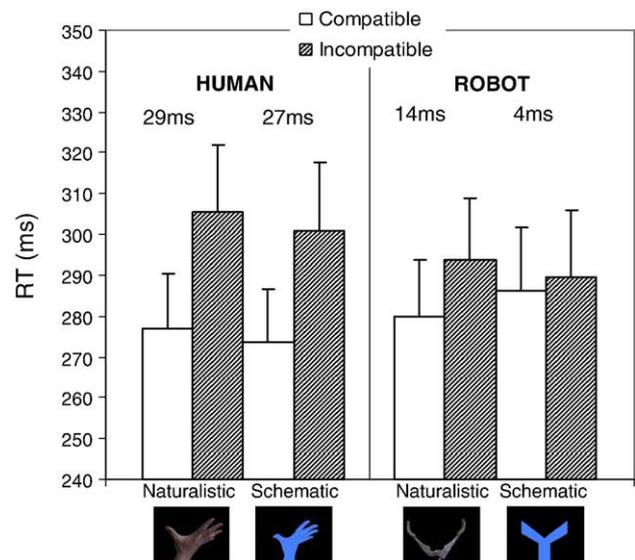

Fig. 2. Mean RT on compatible (open bars) and incompatible (shaded bars) trials for the human naturalistic, human schematic, robotic naturalistic and robotic schematic stimuli. Images on the horizontal axis exemplify stimulus type and style using the open stimulus. Vertical bars indicate the standard error of the mean.

The three-way interaction between compatibility, stimulus type and stimulus style was not significant, $F(1,15) = 3.0$, NS, but, as indicated in Fig. 2, the compatibility effect was smaller for schematic than for naturalistic stimuli of each type. To provide a further check for any differences between the naturalistic and schematic stimuli, data from each stimulus style were analysed separately using ANOVA in which compatibility and stimulus type were the within-Ss variables. Each of these analyses revealed a significant compatibility × stimulus type interaction confirming that, both when the stimuli were naturalistic, $F(1,15) = 8.8$, $P = 0.01$, and when they were schematic, $F(1,15) = 29.8$, $P < 0.001$, the tendency to respond faster on compatible than on incompatible trials was greater when the stimulus hand was human than when it was robotic.

To examine whether the compatibility effect had the same structure for human and robotic stimuli, we performed two supplementary analyses. In the first, the RT distribution was divided into quintiles [32] (Fig. 3). This analysis revealed just one significant effect in addition to those reported above: there was a compatibility × quintile interaction, indicating that the compatibility effect increased with RT ($F(4, 60) = 11.5$, $P < 0.0001$). Fig. 3 suggests that this trend was more sustained when the stimuli were human than when they were robotic, but the compatibility × quintile × stimulus type interaction did not reach significance ($F(4,60) = 3.2$, $P = 0.08$).

The second supplementary analysis examined the development of the compatibility effect in the course of the experiment by including day as a factor. The experiment was conducted over 2 days, and each participant received the same number of trials of each type in the same order on each day. This analysis revealed two significant effects in addition to those reported above: there was a main effect of day ($F(1,15) = 12.7$, $P = 0.003$), indicating that RTs were shorter on day 2 ($M = 273.9$ ms, SEM = 12.3 ms) than on day 1 ($M = 302.8$ ms, SEM = 17.7 ms), and a compatibility × stimulus type × day interaction ($F(1,15) = 4.7$, $P = 0.05$). As indicated in Fig. 4, the compatibility effect for human stimuli was smaller

Fig. 4. Mean RT on compatible (open bars) and incompatible (shaded bars) trials for human stimuli and robotic stimuli on days 1 and 2 of testing. Vertical bars indicate the standard error of the mean.

on day 2 than on day 1, whereas the compatibility effect for robotic stimuli was greater on day 2 than on day 1.

4. Discussion

Previous behavioural and neurophysiological research suggested that the system which mediates visuomotor priming – the mirror neuron, or action observation–execution matching, system – is completely unresponsive to robotic movement stimuli. Using more precise methods of stimulus control, the present study found evidence which challenges this view. The results confirmed that human movement stimuli are more effective visuomotor primes than robotic movement stimuli, but they also showed that robotic movement stimuli can support visuomotor priming; they are sufficient to elicit automatic imitation.

Confirmation that human stimuli are more potent visuomotor primes than robotic movement stimuli came from the compatibility × stimulus type interaction: both when the stimuli were human and when they were robotic, hand movements were executed faster to response compatible stimuli (open stimulus–open response or close stimulus–close response) than to response incompatible stimuli (open stimulus–close response or close stimulus–open response), but this effect of compatibility was greater for human than for robotic stimuli. Previous studies have also found differences between human and robotic stimuli; they have reported that observation of human movements, but not of robotic movements, supports visuomotor priming [7,14,27,28,39], However, these differences could have been due to nonspecific effects on attention. For example, the human stimuli used in previous studies may have been larger, brighter, more colourful and/or more variable than the robotic stimuli with which they were compared.
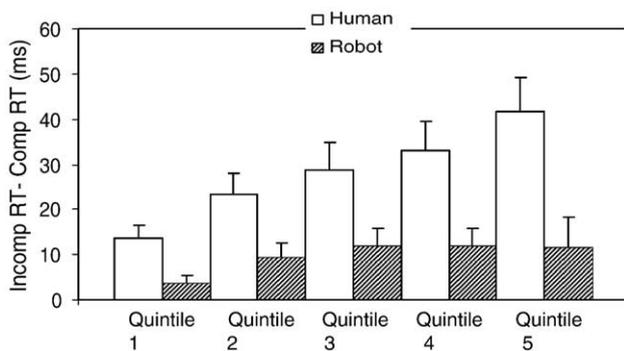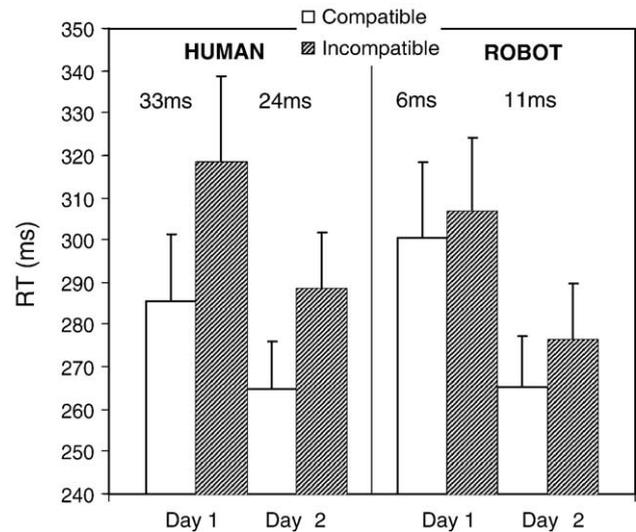

Fig. 3. Mean RT on incompatible trials minus mean RT on compatible trials for human (open bars) and robotic (shaded bars) for five segments of the RT distribution. Vertical bars indicate the standard error of the mean.

Nonspecific attentional effects are very unlikely to have contributed to the human–robot difference observed in the present experiment because it occurred, not only when the human and robotic stimuli varied on a number of dimensions (naturalistic), but also when they differed only in shape (schematic).

In addition to confirming that human movement stimuli are more effective visuomotor primes than robotic movement stimuli, the results provide information about the stimulus dimensions on which this discrimination is based. The human stimuli elicited a stronger automatic imitation effect than the robotic stimuli even when both were represented schematically, i.e. when they differed from one another only in shape. This suggests that variations in kinematic, size, colour, texture and shading cues are not necessary to produce differential activation of the observation–execution matching system by human and robotic stimuli and that variation in shape is a sufficient basis for this discrimination.

The results of the present study provide the first compelling evidence that observation of robotic movement supports visuomotor priming. Responding to response compatible robotic stimuli was faster than responding to response incompatible robotic stimuli. The occurrence of this effect was predicted by the hypothesis that the action observation–execution matching system develops through associative learning [20,22,23,26]. This hypothesis proposes that visuomotor priming of hand movements is mediated by cortical connections formed through experience, primarily self-observation, in which the individual simultaneously observes and executes hand movements. If this is correct, one would expect the effects of this experience to show stimulus generalisation. That is, visuomotor priming by robotic movement stimuli should occur to the extent that those stimuli have visual features in common with human movement stimuli.

The present study was not designed to detect stimulus generalisation via an effect of stimulus style on visuomotor priming; the magnitude of the difference between naturalistic and schematic stimuli was not controlled. However, as one might expect, if the size of the compatibility effect relates to stimulus generalisation, it was numerically smaller for schematic than for naturalistic stimuli of each type.

There are at least two possible reasons why the present study found evidence of visuomotor priming by robotic stimuli whereas previous studies did not [7,14,27,28,39]. First, our robotic movement stimuli may have been more similar in appearance to human movement stimuli. We certainly sought to achieve this effect by matching the robotic to the human stimuli on several dimensions, but, without more detailed information about the stimuli used in previous experiments, it is difficult to make the relevant cross-experimental comparisons. Second, in comparison with the behavioural and neurophysiological measures used in previous studies, the automatic imitation SRC paradigm may be especially sensitive to visuomotor priming and

therefore able to detect even a small priming effect with robotic stimuli.

Both spatial compatibility and 'movement compatibility' effects have been observed in SRC paradigms using body movement stimuli [4]. At the descriptive level, spatial and movement compatibility effects have been distinguished in terms of the stimulus features that are responsible for facilitation of responding on compatible trials and/or interference with responding on incompatible trials. Spatial compatibility effects are due to directional features of the stimuli (left–right, above–below), while movement compatibility effects are due to other nondirectional features that distinguish types of movement, e.g. shape, shading, colour. In spite of this difference at the descriptive level, it is possible that both spatial and movement compatibility effects result from the same processes of learning, in which unidirectional or bidirectional associations are formed between stimulus and response features [1,37,38,42].

Three lines of evidence suggest that the compatibility effects observed in the present experiment were not due to directional features of the stimuli and therefore that they constitute what is known as movement compatibility, visuomotor priming or automatic imitation. First, the directional properties of the human and robotic stimuli were the same, and yet the compatibility effect for the human stimuli was substantially larger than the compatibility effect for the robotic stimuli. Second, whereas spatial compatibility effects tend to decrease as RT increases, the compatibility effects observed in the present experiment increased with RT. Previous studies have shown that movement compatibility effects increase with RT and ascribed this to the fact that nondirectional stimulus features tend to be less discriminable than directional features [4]. Finally, orthogonal compatibility effects in which, for example, down responses are made faster to left than to right stimuli, are not found when, as in the present experiment, responses are made in the left hemispace [8].

We found that the compatibility effect for human stimuli declined slightly across days, whereas the compatibility effect for robotic stimuli was greater on day 2 than on day 1. In both conditions, the compatibility effect was greater for longer RTs, and RTs were shorter on day 2 than on day 1. On this basis, one would expect a decline in the magnitude of the compatibility effect across days not only for the human stimuli but also for the robotic stimuli. However, robotic stimuli are less familiar than human stimuli and are therefore likely to have been more difficult to discriminate at the beginning of the experiment. In this case, the increase in the compatibility effect for robotic stimuli from day 1 to day 2 may have been due to the effects of perceptual learning compensating for those of faster responding.

The associative learning hypothesis, which predicted the results of the current experiment, concerns the developmental origins of visuomotor priming. It suggests that visuomotor priming develops through the operation of task- and

species-general processes of associative learning. In contrast, the simulation hypothesis concerns the function of visuomotor priming. It proposes that visuomotor priming provides a basis for action recognition and for inferences about the mental states of others. These hypotheses are not incompatible. It is possible that the action observation–execution matching system develops through associative learning and that its outputs are used to make inferences about mental states. However, the associative learning hypothesis would conflict with any version of the simulation hypothesis, suggesting that the action observation–execution matching system is an 'innate module' favoured by natural selection because it supports inferences about mental states. Such an hypothesis would imply that, rather than being a product of associative learning, the cortical links mediating visuomotor priming are either innate or arise through a specialised learning process [21].

In conclusion, the findings of the present study suggest that, although it is more responsive to human than to robotic movement stimuli, the action observation–matching system is not tuned exclusively to human input. To varying degrees, we 'simulate' both human and robotic action.

Acknowledgments

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