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HAND TO MOUTH:

AUTOMATIC IMITATION ACROSS EFFECTOR SYSTEMS

ABSTRACT

The effector-specificity of automatic imitation was investigated using a stimulus-response compatibility (SRC) procedure in which participants were required to make an open or a close response with either their hand or their mouth. The correct response for each trial was indicated by a pair of letters, and each of these imperative stimuli was accompanied by task-irrelevant action images depicting a hand or mouth opening or closing. Relative to the response, the irrelevant stimulus was either movement compatible or movement incompatible, and either effector compatible or effector incompatible. A movement compatibility effect was observed for both hand and mouth responses. These movement compatibility effects were present when the irrelevant stimulus was effector compatible and when it was effector incompatible, but they were smaller when the irrelevant stimulus and response effectors were incompatible. These findings, which are consistent with the associative sequence learning model of imitation, indicate that automatic imitation is partially effector-specific, and therefore that the effector specificity of intentional and instructed imitation reflects, at least in part, the nature of the mechanisms that mediate visuomotor translation for imitation.

Keywords: automatic imitation, effector, associative sequence learning (ASL), mirror neuron

Instructed imitation is usually effector-specific. In everyday life and in the laboratory, when a person is asked to imitate an action, they reproduce the trajectory or topography of the modeled movement using the same part of the body. Hand movements are imitated with the hands, foot movements with the feet, and mouth movements with the mouth. The purpose of the present study was to find out whether the effector-specificity of instructed imitation reflects the structure of the core neurocognitive mechanisms of imitation and, if so, what it can tell us about those mechanisms.

A number of studies confirm that, under non-specific imitation instructions, children and adults reproduce modeled movements using the modeled effector system (Franz, Ford & Werner, 2007; Head 1920; Wapner & Cirillo, 1968; Wohlschläger, Gattis & Bekkering, 2003). For example, when an adult model faces a child, says ‘Do this’ or ‘Do as I do’, and raises a hand above his head, the child raises one of her own hands (Wapner & Cirillo, 1968); she does not raise a foot, or an eyebrow. Under these conditions, the laterality of participants’ responses varies with age and task demands. Younger children, and adults under time pressure, tend to imitate right hand movements with the left hand and vice versa (Wapner & Cirillo, 1968; Wohlschläger et al., 2003). Laterality effects of this kind show that instructed imitation performance is flexible with respect to the side of the body used to reproduce the model’s movement, and that it is susceptible to spatial compatibility effects (Bird, Brindley, Leighton & Heyes, 2007, Heyes & Ray, 2004). However, they do not represent a departure from effector-specificity, i.e. imitation of movements using the same effector *system*.

The effector-specificity of instructed imitation may reflect the structure of core mechanisms of imitation, or it may be largely conventional. The core mechanisms of

imitation are those that solve the ‘correspondence problem’ (Brass & Heyes 2005), translating visual input from observed body movements into matching motor output. It is possible that these mechanisms are effector-specific; for example, they may be incapable of translating observed movements of one effector system into motor output in another effector system. If so, then effector-specificity at the mechanism level could be responsible for the effector-specificity observed in instructed imitation performance. Alternatively, it might be that the core mechanisms of imitation are fully or partially effector-independent, and that their output is filtered by cultural knowledge. This hypothesis suggests that, within anatomical constraints, a participant observing a hand movement is enabled by core imitation mechanisms to reproduce the movement with their hand or with an alternative effector system. However, if the participant has been told to ‘do this’ or ‘imitate’, she chooses to use the same effector as the model because she understands these instructions, within the conventions of her language and social group, to require both movement and effector matching.

Studies of imitation in infancy suggest that the effector-specificity of instructed imitation is not purely conventional. In infants too young to be given instructions, observation of tongue protrusion increases the probability of tongue protrusion, but not of lip protrusion (Meltzoff & Moore, 1977; 1983; 1989; 1997). Given the age of the infants in these studies (some as young as 72 hours), it is highly improbable that their behavior was guided by inferences about what was required, or what would be expedient, in the test situation. However, these findings do not provide conclusive evidence that the mechanisms of imitation are effector-specific, because the tendency of infants to respond to tongue protrusion with tongue protrusion may be mediated by arousal processes, rather

than by the mechanisms that mediate imitation later in development (Anisfeld, 1991; 1996; Jones, 1996; 2006; Ullstadius, 1998). The arousal hypothesis is supported by experiments showing that the frequency of infants' tongue protrusion is elevated, not only after observation of tongue protrusion, but also after a comparable period of exposure to flashing lights or lively music (Jones, 1996; 2006).

Like infancy research, some recent studies of 'automatic imitation' in adults provide suggestive, but not conclusive, evidence that the mechanisms of imitation are effector-specific. Performance in automatic imitation tasks is unlikely to be influenced by inferences about the experimenter's expectations or expediency because they examine imitation under conditions in which participants are not told to imitate, may not be aware that they are imitating, and in which imitation can interfere with the execution of task instructions (e.g. Brass, Bekkering, Wohlschläger, & Prinz, 2000; Craighero, Fadiga, Rizzolatti, & Umiltà, 1998; Heyes, Bird, Johnson & Haggard, 2005; Lakin & Chartrand, 2003; Stanley, Gowen, Miall, in press; Stürmer, Aschersleben, & Prinz, 2000). In a study of this kind, Chartrand & Barge (1999) found that, when a model and an observer were in conversation, observation of face rubbing elicited more face rubbing than foot shaking, and vice versa for observation of foot shaking. Similarly, in a choice RT task, Bach & Tipper (2007) asked participants to identify a model as either 'George' or 'John' by pressing a button with their foot or with their hand, and found that observation of the model performing foot actions (kicking a ball) facilitated foot responses, whereas observation of the model performing hand actions (typing on a keyboard) facilitated hand responding. These studies, and others like them (Berger & Hadley, 1975; Bertenthal, Longo & Kosbud, 2007; Brass, Bekkering, Wohlschläger & Prinz, 2000; Gillmeister,

Catmur, Brass & Heyes, in prep), suggest that observation of an effector in motion selectively activates responses made with the same effector. However, they do not tell us whether this ‘effector priming’ effect is specific to movements that match those observed. Therefore, although effector priming is of interest in its own right, its occurrence does not necessarily imply that the mechanisms mediating movement imitation are effector-specific. To find out whether this is the case, it would be necessary to dissociate movement type (e.g. rubbing vs shaking, kicking vs typing) from effector type (e.g. feet vs hands), and to show that observation of a particular movement type is more likely to elicit an imitative response when the response is performed with the modeled effector than when it is performed with an alternative effector. This logic was applied in the present study.

We investigated the effector-specificity of imitation using a stimulus-response compatibility (SRC) automatic imitation procedure (Bertenthal et al., 2006; Brass et al., 2000; Heyes et al., 2005; Kilner, Paulignan, & Blakemore, 2003; Press, Bird, Flach & Heyes, 2005; Stürmer et al., 2000). In each trial of the choice RT task, participants were required to make one of four responses: to open their hand, to close their hand, to open their mouth, or to close their mouth. The correct response for each trial was indicated by a pair of letters presented on a computer screen. The letters were accompanied by one of four, task-irrelevant action stimuli: a photographic image of an open hand, a closed hand, an open mouth, or a closed mouth. Thus, the irrelevant action stimulus and the correct response were either effector compatible and movement compatible (e.g. open hand stimulus and open hand response), effector compatible and movement incompatible (e.g. close hand stimulus and open hand response), effector incompatible and movement

compatible (e.g. open mouth stimulus and open hand response) or effector incompatible and movement incompatible (e.g. close mouth stimulus and an open hand response).

Previous SRC studies, in which all responses were effector compatible, have shown a movement compatibility effect for hand opening and closing responses; e.g. hand opening is initiated faster in response to a hand opening than to a hand closing stimulus (Heyes et al., 2005; Stürmer et al., 2000). They have also shown that this effect is not due to left-right or orthogonal spatial relations between the stimuli and responses (Press, Bird, Walsh, & Heyes, under review). Therefore, in the present study, we expected to find a movement compatibility effect when the stimulus and the response effector were compatible. The primary focus of interest was the relative magnitude of any movement compatibility effect in the effector compatible and the effector incompatible conditions. If imitation mechanisms are effector-independent, rather than effector-specific, then the movement compatibility effect should be equally strong in the effector compatible and effector incompatible conditions. This would be a surprising result, given previous evidence of effector priming, but it would be interpretable, suggesting that the effector-specificity of instructed imitation is conventional or, more broadly, a product of high-level cognitive processes filtering the output from core mechanisms of imitation.

Two theories of imitation, the associative sequence learning model (ASL, Heyes & Ray, 2000; Heyes, 2001) and the active intermodal matching theory (AIM, Chaminade, Meltzoff, & Decety, 2002; Meltzoff & Moore, 1997) predict an interaction between movement compatibility and effector compatibility in the present study. However, whereas the ASL model predicts a smaller but detectable movement compatibility effect

in the effector incompatible condition, the AIM theory apparently predicts the absence of any movement compatibility effect when responses are made with an incompatible effector.

These predictions follow from the assumptions of each theory. The ASL model (Heyes & Ray, 2000; Heyes, 2001) assumes that imitation is mediated by a repertoire of ‘vertical associations’, each linking a sensory representation of an action with a motor representation of the same action. Sensory and motor representations can each include information about the movement and the effector properties of the represented action, and the links between them are acquired in the course of development through associative learning. Their formation depends on correlated experience of observing and executing the same action. Responses that are based on associative learning are known to show stimulus generalization; stimuli that were not present during training elicit the response to the extent that they are physically similar to the training stimuli (Pearce 1987; 1994). Therefore, although it is unlikely that participants will have experienced a reliable correlation between, say, observation of hand opening and execution of mouth opening, the ASL model predicts some facilitation of mouth opening by observation of hand opening because, when they are observed, hand opening resembles mouth opening. For example, both movements involve the separation of two salient objects, the lips in the case of mouth opening, and the fingers and thumb in the case of hand opening.

In contrast with the ASL model, the AIM theory assumes that imitation is a two-stage process: “an imitative act is not one indissociable unit. It can be differentiated into organ [effector] identification and movement components” (Meltzoff & Moore, 1997, p184). The first, ‘organ identification’, stage identifies the effector system used by the

model, leads to generalized activation of the observer's corresponding effector system (effector priming), and to inhibition or 'quietening' of the observer's other effector systems. The second stage, the 'movement component', identifies the movement properties of the modeled action, codes these as 'organ relations' (e.g. 'tongue-to-lips'), and, via this coding, activates or facilitates execution of the same movement by the observer. This model implies that the second stage mechanisms, those that mediate movement imitation, are effector-specific; that they apply effector-specific codes (e.g. tongue-to-lips), and enable matching movements only of the effector system selected at the organ identification stage. Guided by the idea that an imitative act can be dissected into these two components, Chaminade, Meltzoff & Decety (2005) used functional magnetic resonance imaging (fMRI) to show that distinct cortical areas are activated when participants are required to match a modeled effector and to match a modeled movement.

If, as AIM proposes, the movement matching process is based on effector specific codes, then, in the present study, one would not expect an effect of movement compatibility when responses are made with the incompatible effector.

To summarize, we used an automatic imitation SRC procedure to investigate the effector-specificity of the mechanisms that mediate imitation. In this procedure, participants made opening and closing movements of the hand and of the mouth in the presence of task-irrelevant action images that were effector and movement compatible, effector compatible and movement incompatible, effector incompatible and movement compatible, or effector and movement incompatible with the required response. A movement compatibility effect in the effector compatible condition (e.g. faster hand

opening responses in the presence of open than of close hand stimuli) was expected on the basis of previous studies. An equally strong movement compatibility effect in the effector incompatible condition (e.g. faster hand opening responses in the presence of open than of close mouth stimuli), would suggest that imitation mechanisms are effector-independent. A weaker, but significant, movement compatibility effect in the effector incompatible than in the effector compatible condition would indicate that movement imitation is partially effector-specific, and would be consistent with the ASL model of the mechanisms that mediate imitation. The absence of a movement compatibility effect in the effector incompatible condition would indicate that movement imitation is wholly effector-specific, and would be consistent with the account of imitation mechanisms provided by the AIM theory.

EXPERIMENT 1

Participants were instructed to make one of four responses to letters on a computer screen. They were told to open their mouth if the letters were ‘om’, to close their mouth in response to ‘cm’, to open their hand in response to ‘oh’ and to close their hand in response to ‘ch’. Participants were also told that the letters would appear with irrelevant images of hand and mouth movements, which they should ignore. The irrelevant stimuli depicted a hand either opening or closing or a mouth opening or closing. Therefore for any given trial, the response effector was either compatible or incompatible with the irrelevant stimulus effector and the response movement was either compatible or incompatible with the irrelevant stimulus movement. There were therefore

two types of compatibility (effector and movement), and each had two levels (compatible and incompatible).

Method

Participants. Thirteen consenting, healthy participants with an average age of 25.7 years, 7 male, were recruited from the UCL Department of Psychology database and paid a small honorarium for their participation. All were right-handed, had normal or correct-to-normal vision, and were proficient in the English language. They were naïve 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.

Stimuli and apparatus. All stimuli were presented on an LCD laptop computer screen (60Hz, 400mm, 96 DPI) in color on a black background. Viewing was unrestrained at a distance of approximately 600mm. Warning stimuli consisted of photographic images of two effectors side-by-side, a mouth and a right hand, each in a neutral posture (see Figure 1). In half of the trials the hand was on the left of the screen with the mouth on the right, and in the other half, this configuration was reversed.

Each imperative stimulus consisted of the hand and mouth images in the same left-right position as in the preceding warning stimulus, but one effector was displayed in an open or close posture, whereas the other remained in the neutral posture. Additionally, between the effectors, in the centre of the screen, two letters were displayed, one above the other. The letters were in Arial font size 28, lower case, and printed in white on a black background. The two letters combined occupied 1.0° (width) x 2.4° (height) of

viewing angle. The hand and mouth stimuli were matched in terms of overall size of stimulus in the neutral position, size of stimulus when in the open position and size of stimulus when in the close position. In the neutral position, the hand occupied 3.3° (width) x 5.7° (height) of viewing angle and the mouth occupied 3.3° (width) x 5.2° (height) of viewing angle. The distance between the middle finger and thumb when the hand was in the neutral position occupied 1.4° of viewing angle and the distance between the top and bottom lip when the mouth was in the neutral position occupied 1.6° of viewing angle. The distance between the middle finger and thumb when the hand was in the open position occupied 5.2° of viewing angle and the distance between the top and bottom lip when the mouth was in the open position occupied 5.0° of viewing angle. In the close position, the distance between the lips and between the fingers occupied 0° of viewing angle.

There were four letter pairs (ho, hc, mo, mc), each consisting of a letter indicating the correct response effector (h for hand or m for mouth) and a letter indicating the correct response movement (o for open or c for close). In half of the imperative stimuli the letter representing the effector was placed above the letter representing the movement, and in the other half this configuration was reversed.

Figure 1 about here

Data recording and analysis. For both open and close responses, response onset was measured by recording the electromyogram (EMG) from the first dorsal interosseus (FDI) muscle in the hand and the orbicularis oris (OO) in the mouth using

disposable Ag/AgCl surface electrodes. Recording electrodes were placed on the OO on the right hand corner of the mouth and on the FDI on the right hand. Signals were amplified, high-pass filtered at 20Hz, mains-hum filtered at 50Hz and digitised at 2.5kHz. They were rectified and smoothed using a dual-pass Butterworth filter, with a cut-off frequency of 50Hz. Signals were not low-pass filtered. To define a baseline, EMG activity was registered for 100ms when the participant was not moving at the beginning of each trial. A window of 20ms was then shifted progressively over the raw data in 1ms steps. Response onset was defined by the beginning of the first 20ms window after the imperative stimulus in which the standard deviation for that window, and for the following 20ms 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.

Procedure. Each participant was tested individually in a dimly lit room. Participants were told that they would see some pictures of hands and mouths on either side of the screen, but that they should ignore their movements and respond to the letters in the centre of the screen. It was explained that they should open their mouth in response to the letters 'om', close their mouth in response to 'cm', open their hand in response to 'oh' and close their hand in response to 'ch'. Participants were told to make their movement as soon as the letter appeared on the screen but to keep as still as possible at all other times.

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 such that the hand was free to move. The wrist was rotated so that the fingers moved upwards during opening responses and downwards when closing. Participants were shown the correct neutral positions for the hand and the mouth. In the neutral mouth position, participants were required to have their lips slightly parted. They were asked to return to the neutral position after they had made each movement.

All trials began with presentation of the warning stimulus which was replaced 800-2000ms later by an imperative stimulus of 480ms duration. The stimulus onset asynchrony (SOA) varied randomly between 1200 and 2400ms in 400ms steps. After the imperative stimulus the screen went black for 3000ms before the warning stimulus for the next trial appeared.

Each block contained 128 trials in total, 32 trials of each of the four principal types (effector and movement compatible; effector compatible and movement incompatible; effector incompatible and movement compatible; effector and movement incompatible) in random order. In half of the trials of each type, the hand stimulus was on the left of the mouth stimulus, and in the other half it was on the right. Each participant completed two blocks of trials, one in which the effector indicator (h or m) was above the movement indicator (o or c), and the other in which it was below the movement indicator. Half of the participants completed the blocks in the order described, and half in the alternative order. Before testing commenced in each block participants completed 10 practice trials consisting of a random selection of trial types from within that block.

Results and Discussion

Practice trials, incorrect responses (3.9%) and response omissions (3.8%) were excluded from the analysis, as were all RTs smaller than 100ms and greater than 1500ms (0.05%). One participant, for whom more than 10% of the data were missing, was excluded from the analysis. The RT data from the remaining 12 participants are shown in Figures 2 and 3.

Figures 2 and 3 about here

The data were subjected to analysis of variance (ANOVA) in which movement compatibility (compatible and incompatible), effector compatibility (compatible and incompatible), response movement (open and close), and response effector (mouth and hand) were within subjects variables. There were significant main effects of movement compatibility ($F(1,11)=45.1, p<.0001$) and effector compatibility ($F(1,11)=86.0, p<.0001$). Participants were both faster to respond when the irrelevant stimulus movement was response compatible (mean: 752.4 SEM: 24.9) than when it was response incompatible (mean: 788.0 SEM: 27.4), and when the irrelevant stimulus effector was response compatible (mean: 731.8 SEM: 25.7) than when it was response incompatible (Mean: 808.6 SEM: 27.0). There were also significant main effects of response effector ($F(1,11)=32.8, p<.0001$), and of response movement ($F(1,11)=21.7, p<.0001$). Shorter RTs were recorded for mouth responses (mean: 728.1, SEM: 26.6) than for hand responses (mean: 812.3, SEM: 27.6). Shorter RTs were also recorded for open responses (mean: 738.3, SEM: 24.9) than for close responses (mean: 802.1, SEM: 28.8). These main effects may not reflect real reaction time differences but may simply be an artifact

of electrode placement. The FDI muscle may only become active near the end of a close movement but nearer the beginning of an open movement. Similarly the OO muscle may become active nearer the beginning of a mouth open movement than the FDI does during a hand open movement.

The effect of movement compatibility was greater for closing than for opening responses (movement compatibility x response movement, $F(1,11)=5.6$, $p=.04$), but simple effects analysis confirmed that movement compatible responses were faster than movement incompatible responses both when the response was opening ($F(1,11)=11.2$, $p<.006$, compatible: mean: 727.7, SEM 25.4; incompatible: mean: 748.9, SEM: 24.9) and when it was closing ($F(1,11)=27.9$, $p<.0001$, compatible: mean: 777.1, SEM; 26.4 incompatible: mean: 827.1, SEM: 31.8). Similarly, the effect of effector compatibility was greater when responses were made with the hand than when they were made with the mouth (effector compatibility x response effector, $F(1,11)=6.8$, $p=.03$), but effector compatible responses were faster both for mouth responses ($F(1,11)=42.4$, $p<.0001$, compatible: mean 697.6, SEM: 25.8; incompatible: mean: 758.6, SEM: 28.1), and for hand responses ($F(1,11)=69.5$, $p<.0001$, compatible: mean: 765.9, SEM: 27.9; incompatible: mean: 858.6, SEM: 28.3).

Of principal interest, given the purpose of the experiment, there was a significant movement compatibility x effector compatibility interaction ($F(1,11)=5.2$, $p=.044$), indicating that the movement compatibility effect was greater in the effector compatible (52.9ms) than in the effector incompatible (18.2ms) condition. Simple effects analysis indicated a significant movement compatibility effect when the response effector was

compatible with the stimulus effector ($F(1,11)=35.4$, $p<.0001$, but only a trend in this direction when the response effector was incompatible ($F(1,11)=3.5$, $p=.088$).

Thus, the results of the present experiment indicate that automatic imitation is not wholly effector independent. Opening and closing movements of an irrelevant action stimulus had more impact on the speed of opening and closing responses when the responses were performed with the modeled effector (hand responses to hand stimuli, and mouth responses to mouth stimuli) than when they were performed with the alternative effector (hand responses to mouth stimuli, and mouth responses to mouth stimuli). Therefore, they imply that the effector specificity of instructed imitation is not entirely conventional; it is likely to reflect the operation of core imitation mechanisms, and not to be due solely to inferences about what is expected or expedient in the test situation. However, the results of Experiment 1 did not distinguish clearly between the predictions of the ASL and AIM models of imitation. Both models predicted the observed interaction between movement and effector compatibility, but whereas the ASL hypothesis predicted that there would be an effect of movement compatibility in the effector incompatible condition, the AIM model predicted that movement compatibility would not influence performance in this condition. The results showed that movement compatible responses with the incompatible effector were substantially faster than movement incompatible responses with the incompatible effector, but this trend was not quite significant ($F(1,11)=3.51$, $p=.088$).

EXPERIMENT 2

The principal purpose of Experiment 2 was to discriminate more decisively between the predictions of the ASL and AIM models. Therefore, Experiment 2 replicated the basic design and procedure used in Experiment 1, but with an additional sample of participants. Experiment 2 had two further purposes: to check that the movement compatibility effect observed in Experiment 1 was not dependent on spatial compatibility, and to investigate the nature of the effector compatibility effects observed in Experiment 1.

In Experiment 1, hand stimuli moved in a horizontal plane (e.g. the fingers moved to the right of the screen when the hand opened), whereas hand and mouth responses were made in a vertical plain (e.g. the fingers and the upper lip moved upwards when participants made hand opening and mouth opening responses, respectively). Therefore, in hand stimulus trials, the tendency to respond faster on movement compatible trials (e.g. hand or mouth opening in response to a hand open stimulus) could not have been due to spatial compatibility. However, in mouth stimulus trials, up-down spatial compatibility was confounded with movement compatibility. For example, in mouth open stimulus trials, the upper lip of the mouth stimulus moved upwards, and correct responses in the movement compatible condition involved upward movement of the participants' fingers or upper lip. To remove this confound, in Experiment 2 both the hand and the mouth stimuli moved in the horizontal plane. Thus, relative to Experiment 1, the mouth stimulus was rotated 90 degrees anticlockwise from the canonical position, so that the upper lip appeared on the left of the lower lip, and moved towards the left when the mouth stimulus opened. As in Experiment 1, responses were made when the

participant's head was upright. If the movement compatibility effect observed in Experiment 1 was not dependent on up-down spatial compatibility, then it should be replicated in Experiment 2 where up-down spatial compatibility was controlled.

The third purpose of Experiment 2 was to investigate the effector compatibility effects found in Experiment 1. These effects showed that responses with the modeled effector (e.g. hand responses to hand stimuli) were faster, and more susceptible to automatic imitation, than responses with the alternative effector (e.g. hand responses to mouth stimuli). These effects might indicate that observation of an effector system in motion facilitates responding with an anatomically similar effector system, e.g. hand movement observation facilitates hand movements relative to mouth movements. However, these effects might indicate, instead or in addition, that observation of an effector system in motion facilitates responding at body-centered locations typically occupied by that effector system. For example, hand movement observation may facilitate responses made in the typical locations of the hands (e.g. close to the middle of the trunk when seated) relative to responses made in the location of the mouth. To test the anatomical account against the response location account of effector compatibility, Experiment 2 varied the location of the response hand. In the 'far' condition, as in Experiment 1, the participant's responding hand rested on the desk top, just in front of their solar plexus. In the 'near' condition, the participant's responding hand was located directly in front of their mouth. If the effector compatibility effects observed in Experiment 1 were due to the locations of the responding effectors, and not to the anatomical relationship between the stimulus and response effectors, then those effects should be substantially smaller in the near condition than in the far condition.

It is also possible, in principle, that the effector compatibility observed in Experiment 1 was related to the fact that participants could see their hand responses, albeit in peripheral vision, whereas they could not see their mouth responses. To control for this, in Experiment 2 a screen was placed between the participant's body and their responding hand, so that neither hand nor mouth responses were accompanied by visual feedback.

Method

Participants. Twelve additional participants, with an average age of 28.2 years (7 male) were recruited from the same source, and to meet the same requirements, as in Experiment 1.

Stimuli. The stimuli were identical to those in Experiment 1 except that the mouth stimuli were rotated by 90° in an anticlockwise direction from the canonical position, so that the upper lip appeared on the left of the lower lip, and moved towards the left when the mouth stimulus opened. As in Experiment 1, responses were made when the participant's head was upright. Therefore, for both hand and mouth stimuli, the stimulus movement (left/right) was orthogonal to the response movement (up/down).

Procedure. The data recording and analysis were identical to Experiment 1. The procedure was also the same as in Experiment 1, except as follows. Participants completed eight blocks of trials over two sessions, between one and three days apart. Half of the blocks were completed in the 'hand far' position, where, as in Experiment 1, the hand was located approximately 400mm below the mouth. The remaining blocks were completed in the 'hand near' condition, where the participant's right arm lay in a

horizontal position on a raised armrest such that the hand was as close as possible to the mouth in both the horizontal and vertical plane. In both conditions the hand was covered by a rigid black screen so that the participant could not see their hand movements.

Therefore, in Experiment 2, neither hand nor mouth responses yielded visual feedback.

Each block contained 64 trials in total, 16 trials of each of the four principal types (effector and movement compatible; effector compatible and movement incompatible; effector incompatible and movement compatible; effector and movement incompatible) in random order. In half of the trials of each type, the hand stimulus was on the left of the mouth stimulus, and in the other half it was on the right. Each participant completed four blocks of trials on each day, two in which the hand was in the near position and two in which the hand was in the far position. In one 'near' block the effector indicator (h or m) was above the movement indicator (o or c), and in the other near block it was below the movement indicator. This was also the case for the 'far' blocks. The order of presentation of the blocks was counterbalanced. Participants carried out the same four blocks on both days, but on the second day the order of near and far blocks was reversed.

Results and Discussion

Practice trials, incorrect responses (2.9%) and response omissions (3.0%) were excluded from the analysis as were all RTs smaller than 100ms and greater than 1500ms (0.05%). The RT data for the 12 participants is shown in Figures 4 and 5.

Insert Figures 4 and 5 about here

The RT data was subjected to ANOVA in which movement compatibility (compatible and incompatible), effector compatibility (compatible and incompatible) response movement (open and close), response effector (mouth and hand) and hand position (near and far) were within subjects variables. There were no significant main effects or interactions involving the hand position variable. There were significant main effects of movement compatibility ($F(1,11)=58.4$, $p<.0001$), and effector compatibility ($F(1,11)=39.0$, $p<.0001$). Participants were both faster to respond when the irrelevant stimulus movement was response compatible (Mean: 640.4 SEM: 28.4) than when it was response incompatible (Mean: 686.6 SEM 31.6), and when the irrelevant stimulus effector was response compatible (Mean: 633.2 SEM 26.9) than when it was response incompatible (Mean: 693.8 SEM 33.3). There were also significant main effects of response movement ($F(1,11)=7.5$, $p=.02$) and of response effector ($F(1,11)=12.4$, $p=.005$). Shorter RT's were recorded for mouth responses (Mean 644.3, SEM 30.2) than for hand responses (Mean 682.7, SEM 30.6), and for open responses (Mean 650.3, SEM 28.4) than for close responses (Mean 676.7, SEM 32.1).

The effect of movement compatibility was greater for closing than for opening responses (movement compatibility x response movement, $F(1,11)=11.4$, $p=.006$), but simple effects analysis confirmed that movement compatible responses were faster than movement incompatible responses both when the response was opening ($F(1,11)=23.2$, $p=.001$), compatible: mean: 633.2; SEM: 27.6; incompatible: mean: 667.4 SEM: 29.5) and when it was closing ($F(1,11)=69.8$, $p<.0001$), compatible: mean: 647.6 ;SEM: 30.1 incompatible: mean: 705.9, SEM: 34.3). Similarly, the effect of effector compatibility was greater when responses were made with the hand than when they were made with the

mouth (effector compatibility x response effector, $F(1,11)=5.2$, $p=.04$), but effector compatible responses were faster both for mouth responses ($F(1,11)=29.5$, $p<.0001$, compatible: mean: 619.9; SEM 28.0: incompatible: mean: 668.8 SEM: 32.9), and for hand responses ($F(1,11)=32.8$, $p<.0001$, compatible: mean: 646.6; SEM 26.6: incompatible: mean: 718.3, SEM:35.2).

Of principal interest, there was a significant movement compatibility x effector compatibility interaction ($F(1,11)=13.4$, $p=.004$), indicating that the movement compatibility effect was greater in the effector compatible (67.7ms) than in the effector incompatible (24.8ms) condition. Simple effects analysis indicated a significant movement compatibility effect when the response effector was compatible with the stimulus effector ($F(1,11)=64.7$, $p<.0001$, and also when the response effector was incompatible ($F(1,11)=8.7$, $p=.013$).

The results of the present experiment replicated and extended those of Experiment 1. Like Experiment 1, they showed that movement compatibility has less influence on performance when the stimulus and response effectors are incompatible than when they are compatible. Additionally, by controlling for any effects of up-down spatial compatibility on movement compatibility, Experiment 2 confirmed that the hand and mouth movement compatibility effects observed in these experiments were genuine; they were due to the relationship between the stimulus and response actions (opening and closing), and not simply to the elementary spatial properties of these actions. Similarly, by controlling for the possibility that, for example, hand movement stimuli prime movements at canonical hand locations, rather than hand movements *per se*, Experiment 2 confirmed that the effector compatibility effects observed in these experiments were

due to the anatomical, rather than to the spatial, relationship between the stimulus and response effectors. Most importantly, the results of Experiment 2 confirmed that, although the effect of movement compatibility is smaller when the stimulus and response effectors are incompatible than when they are compatible, the movement compatibility effect is significant in the effector incompatible condition. Thus, automatic imitation of movement trajectory occurs even when participants are responding with hand movement to mouth movement stimuli and vice versa. This finding, which was predicted by the ASL model, suggests that the core mechanisms of imitation operate in a way that is partially, but not wholly, effector-specific.

GENERAL DISCUSSION

In everyday life, and in laboratory tasks where participants are instructed to imitate, movements are usually imitated with the modeled effector system, e.g. hand movements are imitated with the hands and foot movement with the feet. To investigate whether this effector-specific tendency in imitative performance reflects the nature of the core mechanisms of imitation, we used a SRC paradigm to investigate the effector-specificity of automatic imitation. The results of two experiments indicated an automatic imitation, or movement compatibility, effect both when participants responded with the modeled effector system (effector compatible condition) and when they responded with an alternative effector system (effector incompatible condition), and that the movement compatibility effect was smaller when an alternative effector was used. More specifically, opening and closing movements of an irrelevant action stimulus had more impact on the speed of opening and closing responses when the responses were

performed with the modeled effector (hand responses to hand stimuli, and mouth responses to mouth stimuli) than when they were performed with the alternative effector (hand responses to mouth stimuli, and mouth responses to mouth stimuli).

Previous studies have demonstrated movement compatibility effects for hand opening and closing stimuli when the stimulus and response effectors were compatible (Heyes et al., 2005; Press et al., 2005; Stürmer et al., 2000), but this study shows for the first time 1) that opening and closing mouth movements are susceptible to automatic imitation, 2) that automatic imitation of opening and closing movements of the hand and mouth transfers across these effector systems, and 3) that the transfer is incomplete; automatic imitation of opening and closing movements of the hand and mouth is partially effector-specific. .

As its name suggests, automatic imitation is likely to be less susceptible to cognitive control than imitative performance based on instructions or endogenously generated intentions (Press, Gillmeister & Heyes 2006). Therefore, the effector-specificity of automatic imitation observed in the present study suggests that, in instructed imitation tasks and in everyday life, participants do not imitate with the modeled effector purely because they judge effector matching to be conventional or expedient. Rather, it suggests that the effector-specificity of imitative performance reflects the structure of the core neurocognitive mechanisms of imitation; the mechanisms that solve the ‘correspondence problem’ (Brass & Heyes, 2005) by translating visual input from observed body movements into matching motor output.

The active intermodal matching theory (AIM, Meltzoff & Moore, 1997) suggests that the mechanisms that solve the correspondence problem operate in two stages. The

first stage identifies the modeled effector, and, when it is completed, the second stage codes the movement performed by that effector. This account implies that the mechanism mediating movement imitation, operative in the second stage, is strictly effector-specific; that it represents the modeled movement in codes that apply exclusively to the modeled effector. If this is correct, then the AIM model is not consistent with the results of the present study, which indicated only partial effector-specificity of automatic imitation.

In contrast, the findings of the present study are consistent with the associative sequence learning (ASL, Heyes & Ray, 2000; Heyes 2001) model of imitation, which suggests that visual input from the model is translated into motor output by a set of bidirectional, excitatory links connecting visual and motor representations of the same action components. These ‘vertical associations’ are thought to be established through associative learning; formed on the basis of correlated experience of observing and executing action components. Because stimulus generalization is a ubiquitous feature of associative learning (Pearce, 1994), the ASL model assumes that vertical associations are activated, not only by the stimuli experienced during learning, but also by other stimuli to the extent that they have physical characteristics in common with the learned stimulus (Press et al., 2005; 2006). Therefore, if the ASL hypothesis is correct, one would expect some facilitation of mouth opening by observation of hand opening, and vice versa, given the visual similarity between the opening movement of a mouth and the opening movement of a hand. Consistent with this prediction, our results indicated partial effector-specificity, a smaller but significant movement compatibility effect when the stimulus and response effectors were incompatible.

Partial effector-specificity of imitation is also consistent with ideomotor theory and the theory of event coding (Greenwald, 1970; Hommel, Musseler, Aschersleben & Prinz, 2001; Prinz, 1997; 2002), which suggest that actions are represented in terms of their sensory consequences, and that action observation primes performance of the same action to the extent that the observed and executed actions have similar sensory consequences. This view can readily explain automatic imitation of hand movements because they are perceptually transparent, i.e. they yield similar visual effects when observed and executed. Automatic imitation of mouth movements, which was demonstrated in adult participants for the first time in the present study, is harder to reconcile with ideomotor theory. This is because mouth movements are perceptually opaque; they yield dissimilar sensory input when observed and executed. For example, when I open my mouth I do not receive any distinctive visual input, but when I observe someone else opening their mouth, I see the lips parting and forming an oval shape. However, ideomotor theory is able to explain imitation of perceptually opaque actions, and partial effector-specificity of automatic imitation, when it is combined with the hypothesis, central to the ASL model, that actions acquire their ‘common’, sensory codes through associative learning (Elsner & Hommel, 2001; 2004). Associative learning allows perceptually opaque actions to be represented by sensory effects which are dissimilar to the direct effects of action execution, but which have been reliably correlated with action execution. For example, although the sight of an opening mouth is not a direct and anatomically inevitable consequence of my opening my mouth, I may learn to represent my mouth opening movement from a third party perspective as a result of being imitated, or looking in a mirror, while performing this action (Heyes & Ray,

2000). Experiences of this kind establish the third party perspective as part of the representation of the executed action, and thereby allow ideomotor theory to invoke the principle of similarity to explain both automatic imitation of perceptually opaque actions, and the partial effector dependence observed in the present experiments.

It is likely that, at the neurological level, imitation is mediated by cortical areas with ‘mirror’ properties; areas that are active both when an action is passively observed and when the same action is executed without visual feedback (e.g. Iacoboni, Woods, Brass, Bekkering, Mazziota, & Rizzolatti, 1999). ‘Mirror neurons’, single units with these visuomotor properties, were first discovered in the premotor and parietal cortices of macaques (e.g. Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Keysers, Kohler, Umiltà, Nanetti, Fogassi, & Gallese 2003; Rizzolatti, Fadiga, Gallese & Fogassi, 1996), and there is now a substantial body of evidence suggesting that there are analogous or homologous areas in the human brain. These studies have revealed mirror areas of premotor and parietal cortices that are sensitive to movement type – active when a movement with a particular topography or trajectory is observed and executed (Gallese et al., 1996; Rizzolatti et al., 1996), and to effector type – active when a movement involving a particular effector is observed and executed (Aziz-Zadeh, Maida, Zaidel, Mazziotta & Iacoboni, 2002; Buccino, Binkofski, Fink, Fadiga, Fogassi, Gallese, Seitz, Zilles, Rizzolatti, Freund, 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000; Watkins Strafella & Paus, 2003; Wheaton, Thompson, Syngeniotis, Abbot & Puce, 2004; Wheaton, Pipingas, Silberstein, & Puce, 2001).

Recent research indicating that the development of mirror areas depends on learning (Calvo-Merino, Glaser, Grezes, Passingham & Haggard, 2005; Cross, Hamilton

& Grafton, 2006; Ferrari, Rozzi & Fogassi, 2005; Keysers et al., 2003), and especially on sensorimotor learning (Catmur, Walsh & Heyes, under review), has promoted the integration of neurological and cognitive models of imitation. More specifically, it has raised the possibility that mirror neurons / areas are formed through correlated experience of observing and executing actions, and therefore that they are the neural correlates of the vertical associations postulated by the ASL model (Heyes 2005, Keysers & Perrett 2004).

In conclusion: The results of the present study indicate that automatic imitation is partially effector-specific: observation of opening and closing movements of the hand and mouth prime execution of corresponding movements by the modeled effector and also by the alternative effector, but the priming effect is smaller when the alternative effector is engaged in responding. This finding, which is consistent with the ASL and ideomotor theories of imitation, suggests that, rather than being conventional, the effector-specificity of intentional and instructed imitation reflects the nature of the mechanisms that mediate visuomotor translation for imitation.

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Authors' note

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Figure Captions

Figure 1. Stimuli depicting (a) the neutral warning stimulus, and (b and c) two examples of imperative stimuli. In Figure 1b the irrelevant stimulus (open mouth) is effector compatible and movement incompatible with the required response (close mouth). In Figure 1c the irrelevant stimulus (close mouth) is effector incompatible and movement incompatible with the required response (open hand).

Fig. 2. Mean RT on movement compatible (black bars) and movement incompatible (grey bars) trials when effector was compatible (left side) and when it was incompatible (right side). Vertical bars indicate the standard error of the mean.

Figure 3. Mean RT for open (diamonds and solid lines) and close (squares and dashed lines) responses for each trial type defined by the stimulus effector (S) and response effector (R) mapping.

Fig. 4. Mean RT on movement compatible (black bars) and movement incompatible (grey bars) trials when effector is compatible (left side) and incompatible (right side). Vertical bars indicate the standard error of the mean.

Figure 5. Mean RT for open (diamonds and solid lines) and close (squares and dashed lines) responses for each trial type defined by the stimulus effector (S) and response effector (R) mapping.

Figure 1

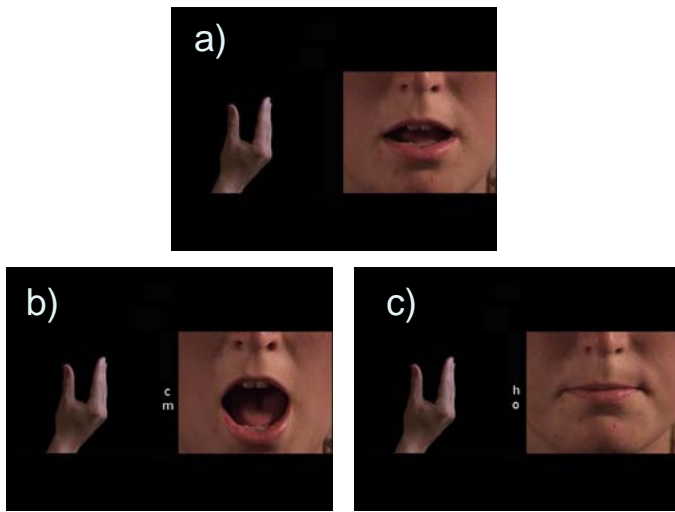


Figure 2

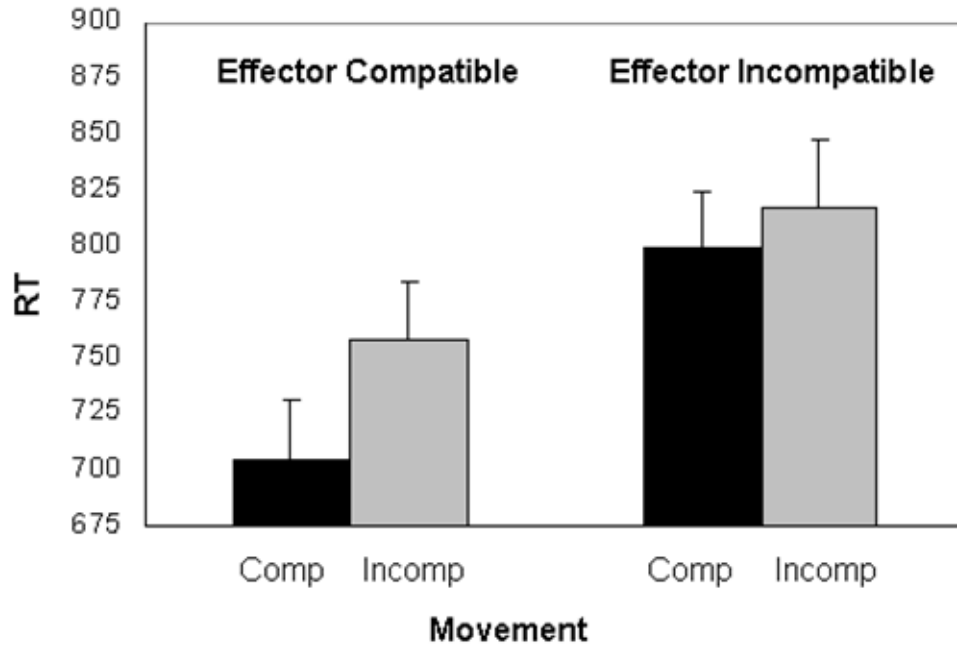


Figure 3

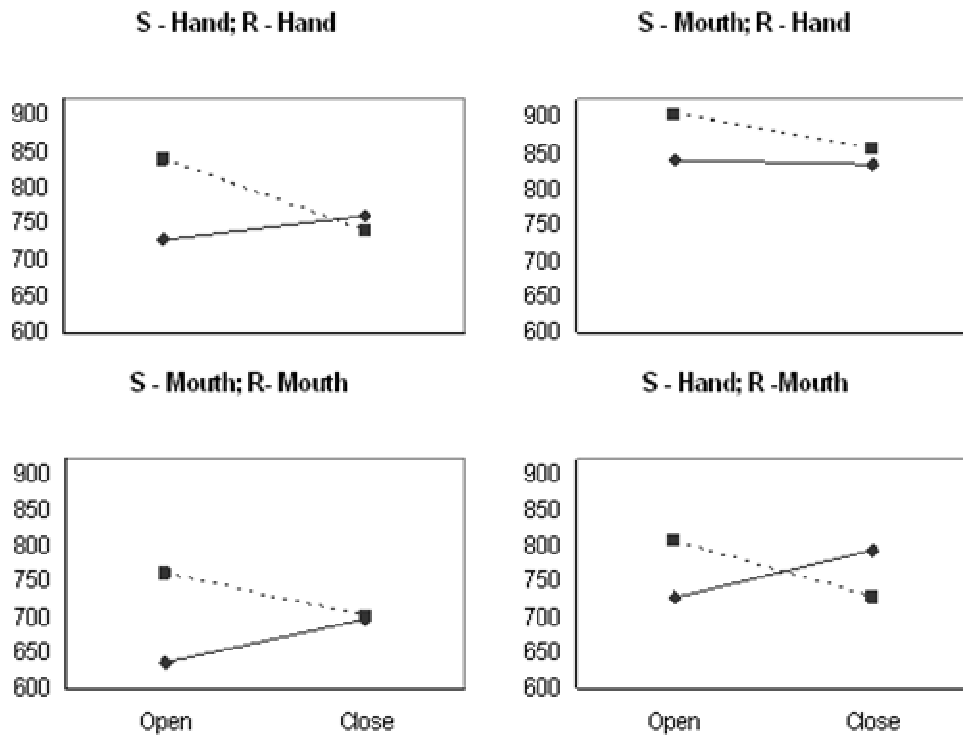


Figure 4

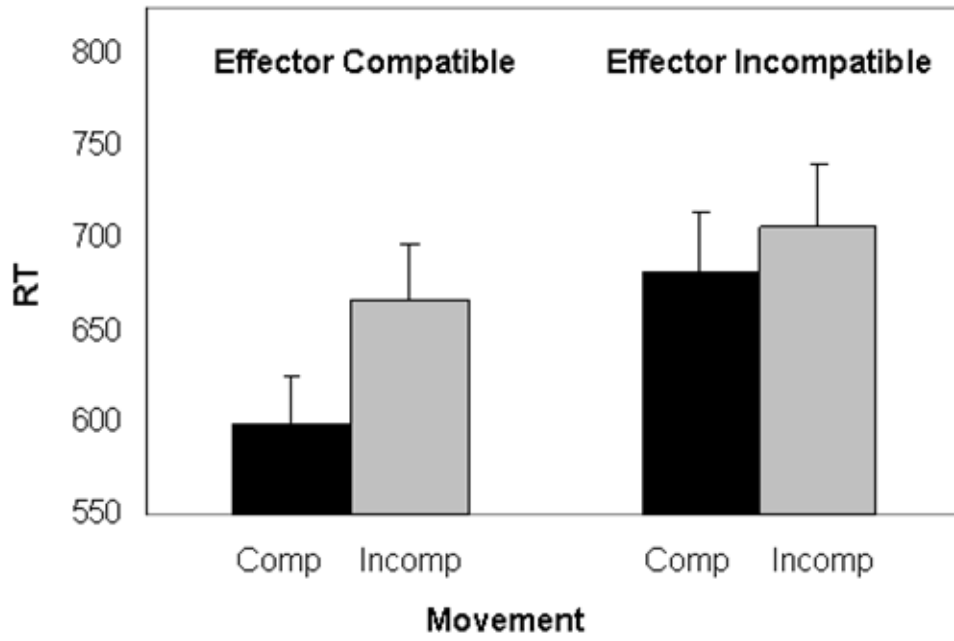


Figure 5

