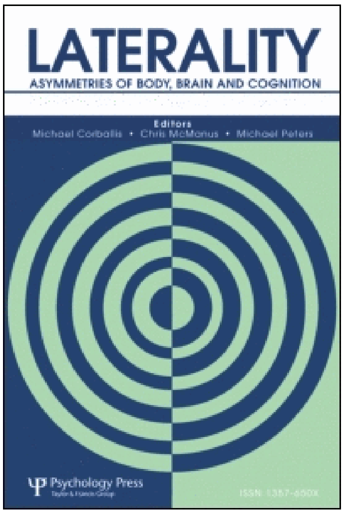

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Imitation of lateralised body movements: Doing it the hard way

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Imitation of lateralised body movements: Doing it the hard way

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Two experiments examined imitation of lateralised body movement sequences presented at six viewing angles (0°, 60°, 120°, 180°, 240°, and 300° rotation relative to the participant's body). Experiment 1 found that, when participants were instructed simply to "do what the model does", at all viewing angles they produced more actions using the same side of the body as the model (anatomical matches), than actions using the opposite side (anatomical non-matches). In Experiment 2 participants were instructed to produce either anatomical matches or anatomical non-matches of observed actions. When the model was viewed from behind (0°), the anatomically matching group were more accurate than the anatomically non-matching group, but the non-matching group was superior when the model faced the participant (180° and 240°). No reliable differences were observed between groups at 60°, 120°, and 300°. In combination, the results of Experiments 1 and 2 suggest that, when they are confronting a model, people choose to imitate the hard way; they attempt to match observed actions anatomically, in spite of the fact that anatomical matching is more subject to error than anatomical non-matching.

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

In motor control, as in other aspects of life, we are apt to choose the path of least resistance; to select among the many actions that *could* be used to achieve a desired outcome those that, by virtue of skill or anatomical constraints, incur the lowest risk of error. For example, I am more likely to use a dexterous hand than a clumsy foot to grasp a small object. However, some disparate findings in the literature on imitation suggest that this principle of efficiency may not be applied when one individual seeks to

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reproduce the body movements of another. Pursuing these findings, the present study asked whether, when it comes to imitation, we choose to "do it the hard way".

We can imitate an observed action (e.g., raising the left arm) using the same effector as an observed model (left arm, anatomically matching), or the corresponding effector on the other side of the body (right arm, anatomically non-matching). If we observe a model from behind (0° rotation), it is intuitively most likely that we will imitate using the anatomically matching effector. However, it is less clear how we will imitate an action if the model is facing us (180° rotation). Developmental data indicate that under these circumstances 8-year-old observers given non-specific instructions (e.g., to "do what the model does") show a strong bias in favour of anatomical non-matching, and that the proportion of anatomically matching responses increases steadily with age until, by adulthood, a strong bias in favour of anatomical matching is observed. Testing imitation of forelimb movements, Gordon (1922/3) reported that the proportion of anatomically matching responses rose from 10% to 50% between the ages of 8 and 13 years, and Wapner and Cirillo (1968) found a bias in favour of anatomical matching at 14, 16, and 18 years, with 80–85% anatomically matching responses in the oldest group.

These developmental data imply that, when adults are given non-specific instructions to imitate a model at 180°, they usually choose to match the models' actions anatomically. However, several other studies suggest that when the model is facing the observer, anatomical matching is less accurate than anatomical non-matching. For example, Ishikura and Inomata (1995) compared adults instructed to match anatomically a sequence of balletic poses at 180°, with adults instructed to non-match anatomically, and found that the anatomical group required more exposures to the modelled actions before they were able to perform the sequence reliably. Similarly, two recent studies have found that when participants were instructed to copy hand and arm actions presented at 180° with the anatomically matching limb, they made more errors than when instructed to copy actions with the anatomically non-matching limb (Avikainen, Wohlschläger, Liuhanen, Hänninen, & Hari, 2003; Franz, Ford, & Werner, 2007).

In combination with the developmental data, these results suggest that when actions are presented at 180° adults prefer to do it the hard way; that they choose to imitate using the anatomically matching side of the body, but are more accurate when using the anatomically non-matching side. However, the inconsistency between the two sets of studies may be due to the fact that they examined imitation of different types of actions. For example, Wapner and Cirillo (1968) were principally concerned with single, object-directed ("transitive") limb movements, whereas Ishikura and Inomata (1995) tested participants using sequences of configural, non-object-directed ("intransitive") limb and body movements, and there is neuropsychological evidence that imitation of transitive and intransitive actions is mediated by distinct mechanisms (e.g., Buxbaum, Kyle, Grossman, & Coslett, 2007).

To find out whether adults really prefer a more error-prone mode of imitation at 180° we used a common set of actions to assess both preference and accuracy. Because of the risk of ceiling effects when studying imitation in a neurologically healthy sample, we presented demanding, seven-item sequences of lateralised head, arm, and leg movements. Experiment 1 tested whether adults show a spontaneous bias in favour of anatomical matching over anatomical non-matching by instructing participants simply to "do what the model does" and counting the number of anatomical matches and non-matches. Experiment 2 compared the accuracy of a group instructed to match anatomically (Group Anat) with the accuracy of a group instructed to non-match anatomically (Group Non-Anat).

The sequences of stimulus actions were presented not only at 180°, but also at 0° (the observer views the model from behind) and, in clockwise rotation, 60°, 120°, 240°, and 300°. The purpose of this variable was to find out whether anatomical matching is more accurate, if not at 180° then across a range of viewing angles. If so, any tendency for "inefficient" anatomical matching at 180° might be explained by over-generalisation of a task-set that is efficient at other angles.

EXPERIMENT 1

Participants observed action sequences and were instructed simply to "do what the model does". This instruction was chosen because it does not specify whether participants should use anatomical matching or non-matching and therefore allowed us to examine spontaneous preferences. This instruction also created an ecologically valid situation (e.g., it is similar to the instructions given in sports and dance classes), and replicated the instructions given to participants by Gordon (1922/1923) and Wapner and Cirillo (1968). The number of correct responses that each participant produced using the anatomically matching, and anatomically non-matching, side of the body was compared at each of six viewing angles (0°, 60°, 120°, 180°, 240°, and 300°). Half of the participants were presented with videos of a human model, and half were presented with computer graphic stimuli. We varied the presentation format in this way because some studies using functional magnetic resonance imaging (fMRI) have suggested that the neural mechanisms mediating imitation are differentially sensitive to "real" and "virtual" action stimuli (e.g., Perani et al., 2001, but see also Maruishi et al., 2004).

Method

Participants. A total of 20 consenting, healthy volunteers, with ages ranging between 19 and 42, of whom 9 were 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.

Stimuli. The videotape action stimuli were modelled by a 26-year-old male of medium build wearing close-fitting black garments, filmed against a white background. The computer graphic stimuli were prepared using 3D Studio software on Windows 95 (see Figure 1). Each seven-item sequence lasted approximately 15 seconds. The video model's image was approximately 1 m high on a wall-mounted screen, and the computer graphic model's image was approximately 0.15 m high on a visual display unit. The actions in each sequence were drawn in random order without replacement from a set of 10 movements. The end-point of each of these movements is shown in Figure 1. There were seven items in each sequence, and six sequences within each block. The first sequence in each block was at a different viewing angle, and the viewing angles in the five subsequent sequences were presented in clockwise succession, e.g., 240°, 300°, 0°, 60°, 120°, 180°, to enhance ecological validity; when watching a dance teacher for example, viewing angle changes predictably as the model rotates his or her body.

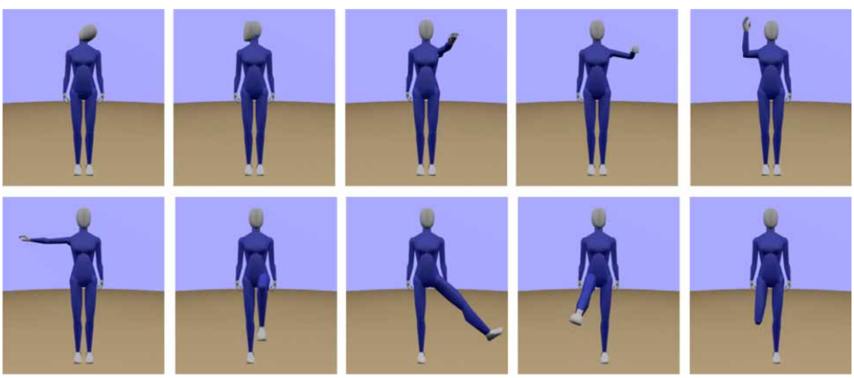

Figure 1. The set of 10 modelled action items in computer graphic format. Actions on videotape appeared similar. Top, left to right: Tilt head left, turn head right, left arm forward straight, left arm back straight, right arm forward bend. Bottom, left to right: Right arm side straight, left leg forward bend, left leg side straight, right leg forward straight, right leg back bend.

Procedure. Participants were tested individually. They stood directly facing the screen at a distance of 2.5 m (video group) or 1.5 m (computer graphic group). Each participant was told that they would be shown a number of action sequences and required to "do what the model does". They were told to wait until each action sequence had finished, to imitate as many items in the sequence as they could, in order, and then to indicate to the experimenter that they were ready to begin the next trial. There were six blocks and the order of blocks was randomised for each participant.

Each participant's performance was videotaped and scored by a person who was blind to the purpose of the experiment. The participant's performance in each trial consisted of a sequence of actions. Each action in the sequence was scored as correct if it matched one of the seven actions modelled in that trial, irrespective of laterality and sequence position. For example, if "left arm straight back" appeared anywhere in the modelled sequence, the participant was scored as having made a correct response if they moved their left *or their right* arm straight back at any point in the response sequence. Correct responses were then subdivided into anatomically matching (in the foregoing example, *left* arm straight back) and anatomically non-matching (*right* arm straight back) responses. The participants did not need to execute the actions in exactly the same manner as the model to be scored as correct; e.g., the action did not need to be of the same duration, the angle of the hand relative to the arm did not need to be identical. If, having observed "left arm straight back", participants moved an arm backwards and their arm was straight, this action was scored as correct. Therefore, there were four error types: omission of an action that had been presented in the target sequence; execution of an action that had not been presented; repetition of a presented action; and execution of an action that could not be identified.

Results and discussion

Figure 2 shows the mean number of items per sequence that were correctly imitated using the anatomically matching, and the anatomically non-matching, sides of the body. These data were subjected to ANOVA in which response type (anatomically matching and anatomically non-matching) and viewing angle (0°, 60°, 120°, 180°, 240°, and 300°) were within-participants factors, and presentation format (video and computer graphic) was a between-participants factor. Where appropriate, a Greenhouse Geisser correction was employed. There were more anatomically matching ($M = 2.66$, $SEM = 0.15$) than non-matching ($M = 1.26$, $SEM = 0.10$) responses, $F(1, 18) = 46.12$, $MSE = 2.53$, $p < .001$, and there was a response type by viewing angle interaction, $F(5, 90) = 7.36$, $MSE = 0.56$, $p < .001$. Simple

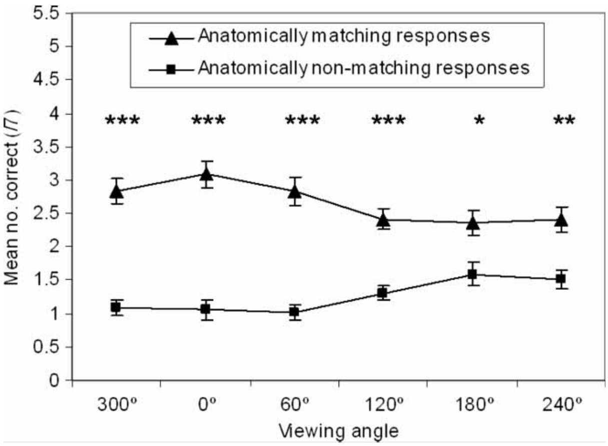

Figure 2. Mean number of action items correctly imitated using the anatomically matching, or non-matching, side of the body, at each viewing angle in Experiment 1. "*", "**", and "***" indicate that the simple effect was significant at $p<.05$, $p<.01$, and $p<.001$, respectively.

effects analyses indicated that more anatomically matching than non-matching responses were made at each angle (see Figure 2), and that this bias was larger when the model was viewed from behind (300°, 0°, and 60°, $M = 1.86$, $SEM = 0.24$) than when the model was facing the participant (120°, 180°, and 240°, $M = 0.93$, $SEM = 0.22$), $F(1, 18) = 19.73$, $MSE = 0.22$, $p < .001$. Equivalent effects were observed at all three angles when the model was viewed from behind (300°, 0°, and 60°), $F(2, 36) = 1.01$, $MSE = 0.26$, $p > .3$, and all three angles when the model was facing the participant (120°, 180°, and 240°), $F(2, 36) < 1$, $MSE = 0.47$, $p > .4$.

Consistent with the findings of Wapner and Cirillo (1968) some 40 years ago, these results indicate that adults show a substantial bias in favour of anatomical matching at all viewing angles, including 180°.

There were no main effects or interactions involving presentation format (all Fs < 1.89, all MSEs > 0.19, all ps $> .12$), implying that our "virtual" model was as effective as the "real" model. This is consistent with a recent report that observation of the movement of prosthetic hands activates the neural mechanisms thought to mediate imitation to the same extent, or to a greater extent, than observation of the movement of real hands (Maruishi et al., 2004). An analysis of error types revealed an error type × viewing angle interaction, $F(15, 270) = 5.38$, $MSE = 0.32$, $p < .001$; for omission errors only, more mistakes were made when the model was facing the participant ($M = 2.03$, $SEM = 0.16$) than when the model was viewed from behind ($M = 1.82$, $SEM = 0.17$), $F(1, 18) = 10.95$, $MSE = 0.04$, $p = .004$.

EXPERIMENT 2

At all viewing angles in Experiment 1, participants who had been asked simply to "do what the model does" produced more anatomically matching than non-matching responses. This suggests that the participants in Experiment 1 preferred anatomical matching at all viewing angles. Experiment 2 sought to investigate whether participants are also more accurate at anatomical matching at all viewing angles, by comparing the performance of participants instructed to match anatomically (Group Anat) with that of participants instructed to non-match anatomically (Group Non-Anat) all observed actions. We used the same action stimuli as in Experiment 1.

Method

A total of 40 consenting, healthy volunteers 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. Two participants were excluded due to a failure to obey task instructions (one from each group), leaving 38 participants with ages ranging between 19 and 48, of whom 18 were male.

The stimuli were the same as those in Experiment 1. Half of the participants were instructed to imitate using the same side of their body as the model (Group Anat), and the other half were instructed to imitate using the other side of their body (Group Non-Anat). Half of each group observed video stimuli and half observed computer graphic stimuli.

Results and discussion

Figure 3 shows, for Group Anat and Group Non-Anat, the mean number of items in a sequence that were correctly imitated using the instructed side of the body. (The instructions for participants in Experiment 2, unlike those in Experiment 1, specified response laterality. Therefore, in Experiment 2 only actions performed using the instructed side of the body were counted as correct.) These data were subjected to ANOVA in which viewing angle (0°, 60°, 120°, 180°, 240°, and 300°) was a within-participants factor, and instruction (Group Anat and Group Non-Anat) and presentation format (videotape and computer graphic format) were between-participants factors. Where appropriate, a Greenhouse Geisser correction was employed. There was a significant instruction × viewing angle interaction, $F(5, 170) = 14.00$, $MSE = 0.36$, $p < .001$. No other main effects or interactions were significant. Simple effects analyses indicated that Group Non-Anat produced significantly more correct responses than Group Anat at 180° and 240°, there was

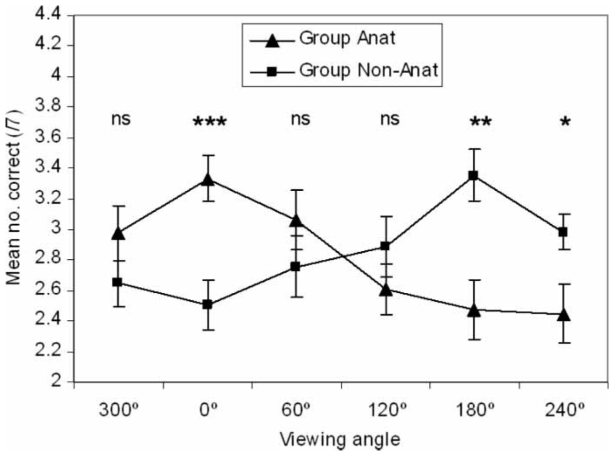

Figure 3. Mean number of action items correctly reproduced according to instructions (anatomically matching in Group Anat or anatomically non-matching in Group Non-Anat), at each viewing angle in Experiment 2. "*ns*" indicates that the simple effect was not significant, and "*", "**", and "***" indicate that the simple effect was significant at $p < .05$, $p < .01$, and $p < .001$, respectively.

no detectable difference between groups at 300° and 120°, and Group Anat produced significantly more correct responses than Group Non-Anat at 0° (see Figure 3).

Figure 4 shows the mean number of lateral reversal errors for Group Anat and Group Non-Anat at each viewing angle. These data were subjected to ANOVA in which viewing angle (0°, 60°, 120°, 180°, 240°, and 300°) was a within-participants factor, and instruction (Group Anat and Group Non-Anat) and presentation format (videotape and computer graphic format) were between-participants factors. Where appropriate, a Greenhouse Geisser correction was employed. In common with the analysis of correct responses, there was an instruction by viewing angle interaction, $F(5, 170) = 9.99$, $MSE = 0.31$, $p < .001$. Simple effects analyses indicated that Group Anat produced significantly more lateral reversal errors than Group Non-Anat at 120°, 180°, and 240°, there was no detectable difference between groups at 300° and 60°, and Group Non-Anat produced significantly more lateral reversal errors than Group Anat at 0° (see Figure 4). Therefore, at those viewing angles where more correct responses were performed in Group Anat relative to Group Non-Anat, fewer lateral reversal errors were made, and at viewing angles where fewer correct responses were performed in Group Anat relative to Group Non-Anat, more lateral reversal errors were made. Thus, the analysis of lateral reversal errors confirms that Group Non-Anat was more accurate than Group Anat at 180° and 240°, and that Group Anat was more accurate than Group Non-Anat at 0°. Furthermore, in combination with the

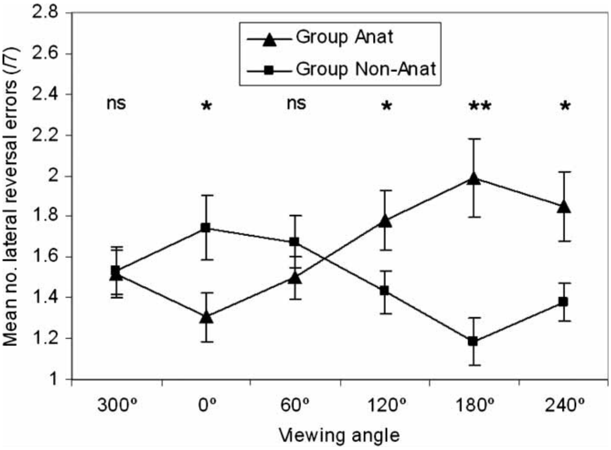

Figure 4. Mean number of lateral reversal errors for each instruction group in Experiment 2. Reversal errors were anatomically non-matching actions for Group Anat and anatomically matching actions for Group Non-Anat. "*ns*" indicates that the simple effect was not significant, and "*" and "**" indicate that the simple effect was significant at $p < .05$ and $p < .01$, respectively.

analysis of correct responses, the lateral reversal error data confirms that the results of Experiment 1—in which participants executed more anatomical matches at all viewing angles—reflected participants' intentions, and not the accuracy with which they were able to implement those intentions.

The finding that, at 180° and 240°, Group Non-Anat produced more correct responses, and fewer lateral reversal errors, than Group Anat is consistent with previous studies which have indicated greater accuracy when participants are instructed to non-match, rather than match, anatomically, actions observed at 180° (Avikainen et al., 2003; Franz et al., 2007; Ishikura & Inomata, 1995). In addition, similarly to Experiment 1, there were no main effects or interactions involving presentation format, consistent with the findings of Maruishi et al. (2004) that prosthetic hands are processed similarly to real hands by the mechanisms mediating imitation.

GENERAL DISCUSSION

Experiment 1 presented participants with sequences of lateralised body movements at 0°, 60°, 120°, 240°, and 300° rotation relative to their own body, and simply instructed them to "do what the model does". It found that, at all viewing angles, participants produced more actions with the anatomically matching, rather than non-matching, side of the body. Experiment 2 presented participants with the same stimuli, but instructed one group (Group Anat) to imitate using the same side of their body as the model, and another group to imitate using the opposite side (Group Non-Anat). This experiment found that, at 180° and 240°, Group Non-Anat were more accurate than Group Anat; at 60°, 120°, and 300° there was no detectable difference between groups; and at 0°, Group Anat were more accurate than Group Non-Anat.

The results of the present study, which used a common set of action stimuli to investigate both choice and accuracy in imitative performance, are consistent with those of a disparate collection of previous studies. Experiment 1 replicated the findings of Wapner and Cirillo (1968) showing that, when a model is viewed at 180°, adult participants show a bias in favour of imitating an observed action using the anatomically matching, rather than non-matching, side of the body. Experiment 2 replicated previous studies showing, in contrast, that participants are more accurate in anatomical non-matching than in anatomical matching at 180° (Avikainen et al., 2003; Franz et al., 2007; Ishikura & Inomata, 1995). This finding is also in line with those of a recent fMRI study investigating cortical activation during anatomical matching and non-matching. Koski, Iacoboni, Dubeau, Woods, and Mazziotta (2003) found that when participants imitated finger actions presented at 180° in an anatomically non-matching fashion there was greater activation of the neural mechanisms thought to mediate imitation than when they imitated the actions in an anatomically matching fashion. The authors took this to indicate that, at 180°, anatomical non-matching relies more heavily than anatomical matching on the mechanisms mediating imitation.

To create an ecologically valid context, the participants in Experiment 1 were instructed simply to “do what the model does”. As in everyday life, where an expert says to a novice “Do as I do” or “Do it this way” before a demonstration, this instruction implicitly offers participants a choice between anatomical matching and anatomical non-matching. The results of Experiment 1 show clearly that, under these conditions, participants select anatomical matching more often than anatomical non-matching. However, they leave open the question of whether this bias depends on explicit processing of the choice between anatomical matching and non-matching. If the same pattern of results were obtained with an explicit choice instruction, in which participants are told that they are free to match with the same or the opposite side of the body, it would suggest that the matching bias is likely to depend on explicit processing of choice.

The finding that participants spontaneously choose to “imitate the hard way” at 180° has obvious implications for skill training regimes that involve imitation. For example, it suggests that an instructor teaching a student how to swing a racquet should not stand opposite the student while expecting them to “do as I do”. If it is not possible for the instructor to execute the action such that the student should copy non-anatomically, they should stand at a different angle of rotation relative to the student.

The tendency to be more accurate when anatomically matching at 0°, but more accurate when anatomically non-matching at 180° and 240°, can be understood with reference to the associative sequence learning (ASL) model of imitation (Brass & Heyes 2005; Heyes 2001; Heyes & Ray, 2000). This model suggests that imitation mechanisms develop through associative learning, and that the learning process is driven by experience in which specific actions—those to which the mechanism will subsequently be responsive—are concurrently observed and executed. Experience of this kind is obtained through self-observation, socially synchronous action, and when the individual is being imitated by others. Experience of observation of action at 180° is likely to be correlated with execution of anatomically non-matching actions, more than anatomically matching actions, because this is the viewing angle typical of mirror self-observation. In contrast, observing at 0° and simultaneously executing anatomically matching actions, is likely to be more common than simultaneously executing anatomically non-matching actions because, for many actions, it can be derived from direct self-observation. (Although we are unlikely to observe our own whole body movements at 0°, we may often observe ourselves performing components of these actions, e.g., a forearm moving forward.) Furthermore, when we are observing another person from behind, we are likely to be concurrently performing actions with the same side of our body, e.g., in an exercise class.

Alternatively, simple left–right spatial compatibility may explain why anatomical non-matching is more accurate at 180° and 240°, whereas anatomical matching is more accurate at 0° (Heyes & Ray, 2004). It is well known that actions are executed faster and more accurately in response to inanimate stimuli that are in the same left-right spatial location as the response hand (see Umiltà & Nicoletti, 1990), or that appear to move towards the response hand (Bosbach, Prinz, & Kerzel, 2004). Spatial compatibility and imitation effects may result from similar processes of learning, in which unidirectional or bidirectional associations are formed between stimulus and response features (e.g., Tagliabue, Zorzi, & Umiltà, 2002). However, there is some evidence to suggest that they are mediated by distinct mechanisms. The mechanisms mediating imitation are thought to reside predominantly in ventral premotor and inferior parietal cortices (Rizzolatti & Craighero, 2004), whereas the mechanisms mediating spatial compatibility may be located in dorsal premotor and posterior parietal cortex (Koski, Molnar-Szakacs, & Iacoboni, 2005).

The results of our study indicate that when confronting a model (180° and 240°), adult participants choose to imitate the hard way; they try to match the model's actions anatomically, in spite of the fact that anatomical matching is more error-prone than anatomical non-matching under these conditions. Why? The accuracy data we obtained at other viewing angles begin to provide an answer. There was no difference in the accuracy of anatomically matching and non-matching imitation at 300°, 60°, and 120°, and anatomically matching imitation was, in fact, more accurate at 0°. Therefore, across viewing angles, any task set or culturally defined convention to match anatomically an observed action will rarely be detrimental, and will sometimes even be beneficial.

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