

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****Brain and cognitive processes of imitation in bimanual situations: Making inferences about mirror neuron systems**

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ABSTRACT

The relationship between mirror neuron systems and imitation is being widely studied. However, most if not all, studies on imitation have investigated only the mirror mode. The present study examined whether imitation in a mirror (specular) mode is likely to reflect similar or distinct neural processes and psychological principles as imitation in a non-mirror (anatomical) mode. Experiment 1 examined whether altering sensory information may reverse the typical mirror mode advantage, resulting in superior performance in the non-mirror mode. Experiment 2 examined whether the two different modes of imitation rely differentially on target selection (goals) and effector selection (means). Experiment 3 examined whether spatial translations are likely to occur in a typical non-mirror imitation mode. Experiment 4 examined whether non-mirror imitation would be the naturally selected mode of imitation under some situations. Findings from all experiments demonstrated marked differences between mirror and non-mirror modes of imitation. The implications of these findings may raise challenges for theories and models of mirror neurons.

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1. Introduction

The last decade has witnessed a rapid proliferation of research on the topic of human imitation, following landmark neurophysiological studies that demonstrated in monkeys the existence of specialized 'mirror neurons' that respond to both action observation and execution (Pellegrino et al., 1992; Rizzolatti et al., 1996). Understanding the principles of imitation seems a crucial step toward learning the precise role of mirror neuron systems in imitative processes. The present study attempts to elucidate the principles that underlie imitation in specular (mirror) and anatomical (non-mirror) response modes. As will be discussed below, virtually no studies have made direct comparisons between these two modes; thus, present theories and models reflect primarily the

principles underlying mirror imitation. Following a brief review of the relevant literature, four experiments will be presented that test hypotheses aimed at elucidating critical similarities and differences in mirror and non-mirror modes of imitation. The findings are then discussed in terms of possible challenges for mirror neuron accounts.

Before the discovery of mirror neurons, experimental studies on humans focused primarily on the development of imitation in infants (Meltzoff and Moore, 1977; Schofield, 1976; Wagner and Cirillo, 1968). One of the initial studies by Meltzoff and Moore (1977) reported that very young infants are much more likely to produce a particular gesture (e.g., a tongue protrusion) if that same gesture was just produced by the experimenter, than if a completely different gesture was previously shown. The theory they proposed to account for

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these findings is that humans have an inborn ability to match visually perceived input of movement with proprioceptive (but not necessarily seen) sensations of the same movement in one's self. More recent electrophysiological and neuroimaging studies have provided indirect evidence of an analogue mirror neuron system in humans that includes a network of brain areas in occipital, temporal, and parietal visual areas in addition to rostral regions of the inferior parietal lobe and part of Broca's area (Grafton et al., 1996; Decety et al., 2002). Notably, the initial work in monkeys suggested that mirror neurons were selective for goal-directed transitive actions. Thus, although the monkeys were able to emulate the goal of actions performed on real or unseen (virtual) objects, they did not necessarily imitate by identical means (Byrne, 2002; Rizzolatti et al., 2002). Contrary to studies on monkeys, the human mirror system appears to code not only the goals of actions but also the means for achieving those actions.

Support for the coding of goals in human imitation dates back to the classic studies by Head. Head (1920) examined imitation of hand movements made to a point in space or an object such as a body part (e.g., grasping the ear) or an object external to the body (e.g., reaching to a colored dot). In these studies, young children (the precise age varying somewhat across studies) more often than older children or adults, tended to produce ipsilateral hand movements to reach an object when imitating what was presented by a model as a contralateral (crossed) movement of the other hand to that same object (Schofield, 1976; Kephart, 1971; Wagner and Cirillo, 1968; Bekkering et al., 2000). More recent studies (Bekkering et al., 2000) employed a modified version of Head's task (to include bimanual responses), and also incorporated variants of object goal manipulations that were initially introduced by Wagner and Cirillo (1968). Specifically, Bekkering et al. attempted to manipulate the saliency of different goals to address the assumption that goals guide the current action plans. In all experiments, Bekkering et al. encouraged use of the mirror (specular) mode by telling children to act as though they are looking in a mirror, given young children tend to naturally imitate in a mirror mode (in contrast to a non-mirror, anatomical mode). Their studies found that error rate was highest when contralateral imitative movements were required (e.g., the correct imitation response would be to move the hand or hands across the midline to touch the ear or ears on the opposite side of the body). On these trials, rather than producing contralateral movements, participants tended to produce ipsilateral movements of the wrong hand(s) to the correct target ear(s). In contrast, imitation of ipsilateral movements tended to be correct on the majority of trials.

In another experiment (Bekkering, et al., Experiment 3), the researchers used as target objects, either two dots or two spatial locations on a table. According to the researchers' logic, the dots would now serve as target objects and therefore would produce behavior similar to that found when the ears were used as target objects. With some exceptions, this prediction was supported, with the dot present condition revealing the highest error in contralateral trials where participants again erred by producing ipsilateral movements. However, nearly 10 percent of ipsilateral trials produced errors of contralateral movements (compared to less than half that amount in Experiment 1), and these ipsilateral errors are difficult to

account for. The researchers claimed that these findings support their hypothesis that when the goal hierarchy is altered by eliminating the dominant goal of the target object (the ears in Experiment 1 and the dots in Experiment 3), the hand choice becomes the dominant goal, supporting a hierarchy of goals. Perhaps it is also worth considering that both the ears and pairs of dots constitute nearly bilaterally identical and visually symmetrical objects (with respect to a reference midline). Thus, it is possible that experiments using some form of bilateral symmetry will demonstrate important principles of imitation that cannot be discerned solely on the basis of tasks employing single objects (e.g., point to your nose) or locations in space. As we will demonstrate in the present study, the use of bilateral targets and choice of effectors making up a bilateral system (left versus right hands) reveal some important differences between the mirror mode (which has been tested extensively) and the non-mirror mode, which has received relatively little empirical investigation so far. As we will show, although goal-directed performance generally occurs under the mirror mode of imitation, this is not necessarily the case for the non-mirror mode (to be discussed below). Moreover, the use of stimulus information (such as dots on either the target locations or the hands) can significantly alter the properties of responding.

Koski et al. (2003) recently used the term anatomical to refer to a non-mirror mode of responding in which a participant imitates a model by moving the anatomically corresponding hand. Consider a task in which a model (experimenter) places her left and right hands, respectively, on left and right home locations, and then moves one hand from its home location to a target located either on a left or right position some distance in front of her body. The participant's task is to imitate the model. Note that there are two modes of imitation that can be used. One is a mirror mode (specular) in which the performer (participant) mimics the model as though looking in a mirror, producing a right hand movement when the model moves her left hand, and a left hand movement when the model moves her right hand. Using the mirror mode, the target choice also is based on a left hand (model) versus right hand (performer) match, and vice versa for the other hand. In contrast, in the non-mirror (anatomical) mode, the performer mimics the model by using the same (anatomically-matched) hand. Interestingly, aside from preliminary comparisons of response mode from one neuroimaging study (Koski et al., 2003) and a very recent laboratory study (Bertenthal et al., 2006, which was brought to our attention during the final review stages of the present paper), the non-mirror mode of imitation and its underlying principles have rarely been investigated. Note too that the two studies that used the non-mirror mode employed finger imitation of one hand. None to our knowledge has employed the use of bilateral choices (left versus right hand choice of movement), to directly compare mirror and non-mirror modes. In our view, without such studies, it is not possible to assess the generality of existing theories and models of imitation. Nor is it possible to evaluate whether the mirror system in humans operates in a similar manner across different imitative tasks. Some current theories of imitation can be considered.

Ideomotor theory, which is based on the notion of ideomotor compatibility as defined by Greenwald (1970), was

particularly influential in the development of theories of imitation. According to Greenwald, ideomotor compatibility reflects the extent to which a stimulus corresponds to sensory feedback associated with the response to that stimulus. Derived from this idea is the closely related ideomotor theory, according to which all actions are represented as images of sensory feedback of the movements they are characterized by (Prinz, 1997). To account for imitation, ideomotor theory posits that a visually observed action activates a representation that then guides a subsequently performed action (Prinz, 2002).

A related (but not identical) class of theories that has been applied to imitation is that of common coding, according to which the same representation is shared by stimuli (e.g., observed stimuli) and responses of actions (Müsseler and Hommel, 1997; Stürmer et al., 2000). With mirror mode imitation, common coding could easily explain situations in which a primed visual stimulus (such as an object) activates a response (e.g., affords an action on that object). Along this logic, studies have been conducted in which objects are placed in a particular orientation and subjects are instructed to grasp them or press keys corresponding to the hand selected to grasp. In these studies, responses are faster when the responding hand is compatible (as opposed to incompatible) with the hand that would normally respond to the object placed in that particular orientation (Tucher and Ellis, 1998). Precisely what properties account for the compatibility, however, has been under debate.

One possibility to account for compatibility is the relation between stimulus sets and response sets, referred to as spatial compatibility (e.g., Brass et al., 2000; Fitts and Seeger, 1953; Hommel and Prinz, 1997; Proctor and Reeve, 1990). Based on spatial compatibility, the spatial location of a stimulus is compatible with the spatial location of a response if both are on the left of a reference, but incompatible if one is on the left and the other on the right. Thus, common coding and spatial compatibility make similar predictions if the dimension of interest (in this case spatial location) is coded and there is overlap between stimulus and response codes (as in the case of left and right). According to either account, reaction time (RT) to produce a binary choice response (of a left or right situated key) to a binary stimulus (located either to the left or to the right of some spatial reference) is faster when the same code describes the position of both the stimulus and response (e.g., compatible) compared to when the stimulus and response are described by different codes (e.g., incompatible). This finding holds for a host of cognitive tasks (e.g., Kornblum et al., 1990; Hommel and Prinz, 1997). Interestingly, all studies on imitation, except the study by Bertenthal et al. (2006) (to our knowledge) have employed only the mirror mode of imitation to examine effects of spatial compatibility and common coding.

A clever series of studies has employed interference paradigms in which a participant observes a movement, usually by viewing a videotape, and that movement provides a 'Go' signal for the participant's own movement. In this situation, although the 'Go' signal is in the form of a visual presentation of a movement representation, the actual response signaled by the 'Go' is predetermined for a block of trials; thus, no real imitation takes place in these tasks. The researchers then measure the latency to respond to the 'Go' signal under conditions in which the perception represented by the 'Go' stimulus is compatible or incompatible with the impending

(albeit predetermined) movement of the participant. Studies using this basic paradigm have consistently reported longer latencies to respond under incompatible compared to compatible trials (Brass et al., 2000; Stürmer et al., 2000). These findings clearly suggest that information associated with perceived movement influences representation of a planned movement, providing support for common coding and ideomotor theories. In addition, extended practice on the incompatible condition has been shown to reduce the planning time costs found on the standard paradigm that uses unpracticed performance (Heyes et al., 2005). These studies therefore provide support for the idea that response priming occurs following visual presentation of actions. However, until recently it was unclear whether such findings provide evidence for an automatic tendency to imitate upon observation of an action (e.g., mediated by a mirror neuron system), or for the influence of spatial compatibility, or both. To clarify this issue, Bertenthal et al. (2006) pitted manipulations of spatial compatibility against automatic imitation and found that while spatial compatibility appeared to be a stronger prime than automatic imitation, both factors contribute to response priming. Moreover, when placed in opposition, the two factors are likely to interfere with one another. The findings of Bertenthal et al. also suggest that response tendencies might not all be based on the same processes. Recent investigations of meaningful and meaningless imitative actions have also pointed to the possibility that strategic control mechanisms might underlie imitation (Tessari and Rumiati, 2004).

In summary, previous research has examined priming in imitation tasks, using primarily the mirror mode of imitation. These studies have provided support for common coding theories which depend on factors of spatial compatibility as well as the activation of certain response tendencies. However, we know of no direct behavioral comparisons between the mirror and non-mirror modes of imitation to address whether the properties underlying these two modes are likely to be similar or distinct. In the present paper, we aim to demonstrate that the mirror and non-mirror modes of imitation reveal marked differences. We propose that these differences should be taken into account in models and theories about imitation and hypotheses about the way mirror neuron systems operate.

In our bimanual imitation task, the subject must imitate the model's movement of one hand to one of two targets. Our pilot tests indicated that when instructions were to imitate the model in the non-mirror (anatomical) mode, participants' reaction times (RTs) (measured from when the model completed her movement to the onset of the participant's movement) were longer than when instructions were to imitate in the mirror (specular) mode. Our initial question (Experiment 1) was whether this natural tendency (or advantage) to imitate in the mirror mode might reverse under certain conditions, such as with the addition of stimulus information. Consider, for example, that both the model and the participant are wearing wedding bands on a finger of the left hand. This form of stimulus information, although irrelevant to the task, could be used by the participant to ease response selection processes because now only the hand with (or without) the ring would have to be matched when the appropriate hand is selected to produce the imitative movement. However, that same form of stimulus information (the wedding band) would potentially

interfere with mirror mode performance because it now becomes a source of distraction rather than an aide to response selection, given a direct mirror match is appropriate for mirror imitation (and this is in conflict with the response tendency provided by the stimulus match).

In Experiment 1, we manipulated mode of imitation in a between-subjects manner by dividing participants into two groups: mirror and non-mirror. The null hypothesis was that the two different modes would produce identical effects. The alternative hypothesis (and our prediction) was that the presence of distinctive stimulus information would reduce RT for response selection in the non-mirror mode so that RT would be faster than in baseline performance (without the presence of markers). We further predicted that for the mirror mode, the use of stimulus distinctiveness information on anatomically matching hands should slow RT because it would conflict with the natural tendency based on a direct mapping provided by the mirror-image match. Thus, our overall prediction was that the non-mirror (anatomical) mode should produce similar or faster RTs than the mirror (specular) mode when stimulus markers were present on matching hands. This novel finding would provide strong support for the view that imitation performance depends critically on the presence of spatial information.

To examine the coding hierarchy, in Experiment 2 participants were tested using either the mirror or non-mirror mode on our bimanual imitation task with certain factors (either hand or target) held constant in different blocks of trials. The logic was that the prioritization of a particular factor (hand or target) should be revealed by the extent to which holding that factor constant influences overall RT. If the two manipulations (holding hand constant versus holding target constant) result in different magnitudes of RT savings, then a clear priority in processing should be apparent. Based on the earlier findings of Bekkering et al. (using a mirror mode only) we hypothesized that participants in the mirror group would prioritize processing of the target. Because the non-mirror mode was not investigated in previous research, it was an empirical question whether the pattern of findings would mimic those of the mirror group. We were particularly interested in the possibility that the non-mirror mode of imitation would show the opposite effect, in that an effector (hand) or means-based coding is more likely to be used, due to the necessity to select the correct hand to respond. Such evidence would suggest that correct response selection in the non-mirror mode is in opposition to the natural tendency to mirror the movements.

Experiment 3 further examined what makes the non-mirror mode different from the mirror mode. One theoretical account that has been proposed to differentiate mirror and non-mirror modes in perceptual discriminations of stimuli, relates to viewer perspective (Neggert et al., 2005). An extension of this account is that when perceiving stimuli from a viewer-centered perspective, if the viewer can align him- or herself with the framework of the stimulus without having to rotate his or her own body representation, then the viewer perspective requires no spatial translation. In contrast, if a rotation of one's own body representation is necessary to align herself with the stimulus, then a spatial translation is required. Whether or not a spatial translation applies to imitation tasks, is not yet known. Logically, it would be the non-mirror

mode of imitation that would require a translation if such spatial translations actually occur. We reasoned that, if subjects were instructed in the non-mirror mode to make such translations, and these translations actually slowed performance, then we would have at least some support for the view that non-mirror (anatomical) imitation does not usually operate via a spatial translation (e.g., the subject acting as though in the shoes of the model). In other words, if what differentiates mirror from non-mirror imitation is a spatial translation process operating in the latter but not the former, then this process should most likely be quite natural when subjects adopt the non-mirror mode.

Experiment 4 examined whether participants can flexibly change from one mode to the other to adapt to task characteristics. In Experiments 1, 2, and 3, participants were divided randomly into two groups, and each group received a different set of instructions (mirror versus non-mirror imitation). This leaves open the important question of what participants would do if given the choice to imitate in either the mirror or non-mirror mode. We hypothesized that the majority of participants would naturally choose to imitate in the mirror mode if no stimulus markers were present (with no other special instructions given). In contrast, we hypothesized that with the presence of anatomically-matched markers (as in Experiment 1), the mirror mode advantage would reverse in some subjects who previously selected the mirror mode. The results of these experiments will now be discussed in turn.

2. Results

2.1. Results 1

Due to the large range of possible variables to report, we limit our results and discussion to only those significant findings that are meaningful and interpretable. Where this is not the case, we will simply mention that no meaningful results were found, and we will refrain from reporting a large catalogue of results that do not address our hypotheses.

A 2×3 mixed-effects repeated measures analysis of variance (ANOVA) on the factors group×condition was applied to each dependent variable of interest. We were not interested in whether the right or the left hand was faster to respond or to move, given the design consisted of equal numbers of right and left hand responses. However, preliminary analyses revealed the expected subtle differences in which the right hand moved slightly faster than the left (for the model and the participants), although this effect was not significant for the participant groups as a whole ($p=0.14$); there were no other handedness effects that approached statistical significance. Accordingly, all analyses we report below are collapsed across the two hands. We also found no significant differences depending on whether the right hand (target) or the left hand (target) was marked, so all analyses report data collapsed across the left and right hands/target markers for marker conditions. Greenhouse-Geisser corrections are reported where appropriate.

2.1.1. Errors

Errors were tallied separately for incorrect hand, incorrect target, and both incorrect hand and target. Table 1 shows

Table 1 – Cumulative errors for the (H)and, (T)arget, and (B)oth hand and target, as a function of task condition and Mir and Non modes of imitation on each experiment

| Error type: | H | T | B | H | T | B | H | T | B |
|--------------|----------|---|----|---------------|---|-----|-----------------|---|-----|
| Experiment 1 | Baseline | | | Hand marked | | | Target marked | | |
| Mir | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Non | 9 | 2 | 28 | 0 | 0 | 36 | 0 | 0 | 33 |
| Experiment 2 | Baseline | | | Hand constant | | | Target constant | | |
| Mir | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 2 | ** |
| Non | 0 | 0 | 17 | 2 | 0 | 0 | 0 | 5 | ** |
| Experiment 3 | Baseline | | | Hands marked | | | Targets marked | | |
| Mir | 0 | 0 | 2 | 0 | 0 | *** | 0 | 0 | *** |
| Non | 0 | 0 | 53 | 0 | 0 | 43 | 0 | 0 | *** |

*In each case, 1 subject switched modes during the block and produced in excess of 45 errors. All other subjects produced 0 errors.

**In each case, 2 subjects switched modes during the block and produced in excess of 42 errors each. All other subjects produced 0 errors.

***In each case, 1 subject switched modes during the block and produced in excess of 43 errors. All other subjects produced 0 errors. Note that in the other conditions with high error counts, the sum of errors is shown across all subjects, and approximately 6 subjects in total made up the cumulative total.

cumulative errors for all subjects in each condition. As can be seen in Table 1, error rate was virtually zero for the Mir group. In the Non group, errors totaled approximately 9% and were random across the different conditions (baseline, hand marked, and target marked), although they were all errors of both hand and target. Analyses on RT, MT, and velocity were conducted on error-free trials.

2.1.2. RT

The grand mean RT across all conditions for both groups combined was 919 ms (SE=54), and there was no hint of a difference between the two groups, $F < 1.00$. Of primary interest, whereas there was only a minimal effect of marking the hand or the target for the Mir group, $F < 1.00$, the effect of a marker was highly significant for the Non group, $F(2,18) = 8.15$, $p = 0.005$. This effect is shown in Fig. 1 for the two groups. As is clearly shown from the figure, there was a very large benefit of marking the hand or the target for subjects performing in the Non mode, whereas, there was virtually no benefit (and even some cost) for subjects performing in the mirror (specular) mode. Planned contrasts confirmed that the condition \times group interaction was highly significant for the baseline versus hand marked condition ($p = 0.009$) and the baseline versus target marked condition ($p = 0.003$), revealing differences only in the Non group. There was no significant difference between the hand-marked and target-marked conditions for the Non group, $F < 1.00$. Thus, our manipulation of placing anatomically matched distinctive markers on the hands was equally beneficial to performance as placing distinctive markers on the targets for participants in the Non group. The similar facilitation found with hand-marked and target-marked conditions, suggests that selection of both the hand and the target occurs during the RT interval, prior to movement onset.

Clearly, the stimulus marker facilitated performance. These findings apply only to the Non group, however. The Mir group demonstrated a slight slowing in speed of responding when the hand or target was marked. However, this slowing was not statistically significant.

2.1.3. MT and velocity

MT did not differ significantly for the two groups, although it was slightly faster for the Mir group on average (mean for Mir group = 516 ms, mean for Non group = 539 ms). MT was also not significantly different across conditions for the two groups combined, $F(2,36) = 1.14$, $p = 0.331$, nor did the group \times condition interaction reach levels of statistical reliability.

The average velocity for both groups was approximately 29 cm/s, and there was no hint of a difference in average velocity for the two groups across all the conditions combined, $F < 1.00$. However, there was a highly significant interaction of condition \times group that revealed a faster velocity for the Mir group on conditions with a marker present (on either the hand or target: mean = 31 cm/s), and a slower velocity for the Non group with a marker present (mean = 27 cm/s), compared to baseline conditions, $F(2,36) = 6.917$, $p = 0.003$. These findings are consistent with a trend shown for MT. Together with the effects on RT, these findings suggest that differences between conditions reflect a trade-off between movement planning/preparation and movement velocity. Specifically, in conditions where subjects took longer to prepare, movements could be executed faster, whereas when less time was taken for preparation, processing appears to have continued into the movement portion, thereby attenuating movement speed.

In summary, this evidence strongly supports our predictions that the presence of stimulus markers that are not related to the task goals, can strongly influence response selection processes. But, this is not always the case. In fact, the pattern of effects depends on the mode of imitation. Clearly, altering the sensory information by adding markers on anatomically matching hands (or on corresponding targets) reversed the typical mirror mode advantage of imitation to an anatomical mode (Fig. 1).

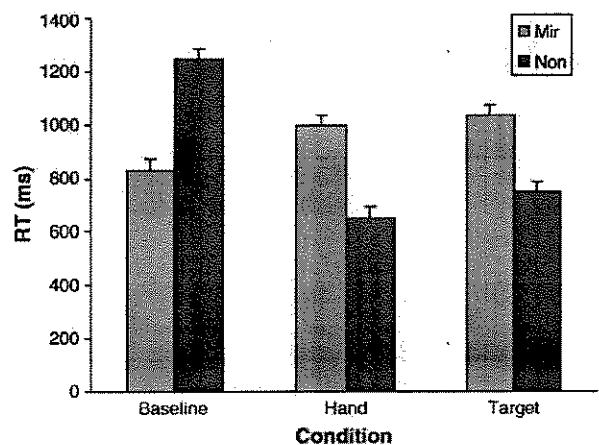


Fig. 1 – Mean RT for Experiment 1 for Mir and Non groups, for the three experimental conditions.

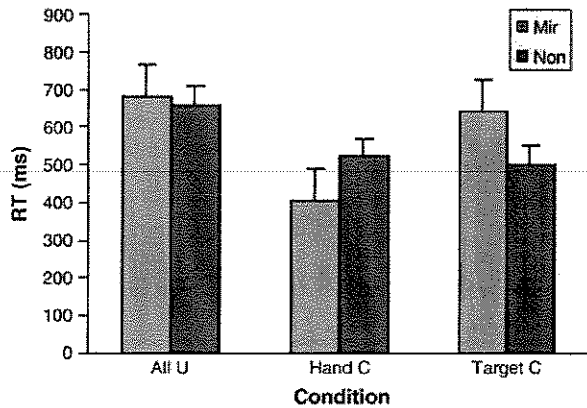


Fig. 2 – Mean RT for Experiment 2 for Mir and Non groups, for the three experimental conditions.

2.2. Results 2

Results are reported for correct trials only on blocks that involved a majority of correct trials (>67 correct out of 72) and a small number of errors (up to 6 errors on a block). In two cases (of the included data), subjects produced virtually no errors on 4 out of the 5 blocks of analyzed trials, and on only one block they reversed performance into the other mode approximately halfway through the block (see Table 1). Obviously, inclusion of these complete or partial block errors in the total count would result in an increased error count. However, that would also represent a very skewed distribution across participants. We therefore avoided any formal analyses on error beyond determining that there were no apparent patterns across conditions ($p > 0.05$) or groups ($p > 0.05$).

2.2.1. RT

The omnibus test on correct trials for all conditions revealed no main effect of Group ($F < 1.00$). However, there was a highly significant effect of condition, $F(2,28) = 7.04$, $p = .003$. As can be seen in Fig. 2, on trials with complete uncertainty, the Mir and Non groups performed approximately the same, on average ($F < 1.00$). Thus, in the context of other uncertainty manipulations, RT was quite similar in the baseline conditions for the two groups. Moreover, the group \times condition interaction was very strong for the remaining two conditions (Hand Certain and Target Certain), with larger RT benefits for the Mir group on hand certain conditions, and larger benefits for the Non-mirror group on target certain conditions, yielding a significant group \times condition interaction, $F(1,14) = 6.08$, $p = 0.027$. These results are consistent with the view that the two groups processed the task with different priorities. The RT facilitation for the Mir group in the Hand Certain condition could be explained by the idea that subjects maximize their performance by paying attention solely to the target positions, keeping behavior consistent with what is most natural. These findings are consistent with Bekkering et al., who also reported that the movement goals are at the top of the hierarchy (and their task employed only the mirror mode). The opposite was found for the Non group in whom a constant target was more beneficial to performance than a constant

hand, suggesting that attention was prioritized to the hand selection process (e.g., means-based) rather than the target selection process, and perhaps suggesting that a means-based processing is most natural. Clearly, task certainty affects the Mir and Non groups differently, and depends on the task and situation.

2.2.2. MT and average velocity

Effects of uncertainty on MT were clear cut. The grand mean was 464 ms ($SE = 16$). There were no significant differences across group or condition, nor did these factors significantly interact (all $p > 0.20$). These findings strongly support the conclusion that uncertainty manipulations of both hand and target affect only pre-movement variables in both the Mir and Non groups. Findings for average velocity closely mirrored those of MT. The grand mean was 33 cm/s, and all averaged values fell within the range of 30–35 cm/s, with no significant main effects or any interaction of group and hand, all $p > 0.20$.

To summarize the results of Experiment 2, findings based on uncertainty manipulations demonstrated that RT for the Mir group was fastest on the hand certain condition, in line with the proposal that performance is maximized under goal (target)-directed processing. In contrast, the Non group's RT was fastest in the target certain condition, as though hand (means/effector)-directed selection processes were primary. The latter effects are novel to the present study. These findings also clearly reveal that manipulations of task uncertainty influence primarily the pre-movement stages and not movement parameters.

2.3. Results 3

All participants in the Non group admitted using the spatial translation strategy, and none in the Mir group did, verifying that participants followed our instructions. Moreover, 80% participants in the Mir group readily admitted that they attempted to ignore the markers altogether.

Cumulative errors are listed in Table 1. As can be seen from the table, very few errors occurred in all conditions for the Mir group. For the Non group, errors occurred primarily on both the hand and target. Due to the skewed distribution of errors, they will not be analyzed further.

2.3.1. RT

Mean RTs are listed in Table 2. As can be seen from these values, the Non group produced significantly slower RTs than

Table 2 – Mean RT (standard error) for each condition in Experiment 3

| Condition | | | |
|-----------|----------|----------|----------|
| Group | Baseline | H marked | T marked |
| Mir | 654 (75) | 699 (75) | 703 (76) |
| Non | 969 (89) | 934 (75) | 959 (76) |
| Dif | 315 | 235 | 256 |

Mir = mirror mode, Non = Non-mirror mode, H = hand, T = target, Dif = difference score (Non-Mir).

the Mir group, on average, $F(1,22)=6.82$, $p=0.016$. These effects contrast with those of the previous experiments, in which there were no main effects of mode (group). There were no other significant effects on RT. It seems clear that when instructed to apply a spatial translation so that the subject is performing the task as though in the model's shoes, overall performance is greatly slowed. Thus, it does not seem to be the natural tendency of subjects in the non-mirror mode to perform a spatial translation in which they align their body representations with the representation of the model (otherwise, RT would not be considerably slowed). There were no meaningful or significant results on MT or average velocity, so those results are omitted.

2.4. Results 4

Although we collected and analyzed RT, MT, and average velocity, these effects have already been reported in earlier experiments, and results would require additional commentary to account for the order effects unveiled by the findings on error and performance mode. Thus, we limit our results and discussion to only error and performance mode for this experiment because they were the important indicators of what subjects spontaneously chose to do. Of the 20 participants tested, 3 produced very high errors (>40%) on at least one condition. We therefore eliminated those participants and analyzed the remaining 17.

Summarized in Table 3 are the numbers of participants who performed in the mirror and non-mirror modes in each of the four conditions. As can be seen from the table, all except 3 participants initially adopted the mirror mode. In subsequent stimulus marked conditions, however, 6 participants who previously imitated in the mirror mode shifted to the non-mirror mode. These findings partially support our predictions (based on findings of Experiment 1), that when stimulus markers are present, facilitation in performance occurs in non-mirror imitation. However, not all participants shifted to the easier non-mirror mode of performance, providing only partial support for a stimulus-based account and partial support for an experience-based account. Of additional inter-

est, participants tended to shift back to the mirror mode in the second baseline condition that followed both stimulus marked conditions. Thus, a number of participants tended to flexibly shift depending on the availability of stimulus markers. One will also note that cumulative error rate was 0 in the mirror mode under all conditions, and was approximately 18 (out of the total 72 per block) for conditions performed in the non-mirror mode, with no obvious patterns across conditions (although the lack of power due to small numbers prohibited any formal analysis of errors). If mirror imitation was easier than non-mirror imitation generally, then one would expect participants to continue to use the mirror mode, even with stimulus markers present, given that those markers provide no information about the certainty of which hand or target will be used on any given trial.

In summary, in the present experiment a significant proportion of participants demonstrated a tendency to shift modes from mirror to non-mirror when the stimulus markers were present, indicating that flexible adaptations to the task and situation do occur.

3. Discussion

The primary purpose of the present study was to directly compare, for the first time, performance variables in mirror and non-mirror modes of imitation in a bilateral choice task, to elucidate whether the principles that apply to the two modes are similar. We build on the theoretical proposal that in imitative tasks that involve a choice of bilateral effectors such as the hands or arms, competing response tendencies exist between a direct matching (e.g., mirror) mode and an anatomical (non-mirror) mode of imitation, and the shift of these competitive response tendencies depends on the task, situation, stimulus information, and instructions.

Our findings from Experiment 1 strongly support the proposal that the use of certain types of stimulus information can reverse the typical mirror advantage, resulting in superior performance in the non-mirror mode of imitation. Experiment 2 addressed a claim made by earlier research by Bekkering et al., namely that a specific goal hierarchy determines the components of the imitation task that the participant primarily processes. Using a mirror mode only, Bekkering et al. reported evidence in support of their claim that the goal (or final target) was at the top of the processing hierarchy (e.g., was of highest priority). Our findings from Experiment 2 are consistent with that claim, based on performance of the mirror group. However, for the non-mirror group, the pattern of RT savings revealed that hand rather than target selection, was of highest priority. Thus, while goal (target)-directed selection tends to occur in the mirror mode, effector (means)-directed selection tends to guide behavior in the non-mirror mode. These novel findings offer strong support for the view that the principles underlying imitation performance are task dependent, as well as dependent on the mode of imitation used.

Findings from Experiment 3 further bolster our claim that different theories and models apply to imitation performance depending on the task and situation. Using an otherwise similar task to Experiment 1, Experiment 3 varied the stimulus information and the instructions to participants to encourage

Table 3 – Number of participants in Experiment 4 who performed in each mode for each condition and (total error count), followed by number of participants who shifted modes in each condition compared to the initial baseline condition

| Condition | Base 1 | T marked | H marked | Base 2 |
|--|--------|----------|----------|--------|
| # Mir mode (error) | 14 (0) | 9 (0) | 9 (0) | 13 (0) |
| # Non mode (error) | 3 (16) | 8 (21) | 8 (20) | 4 (16) |
| Shift: Mir to Non (compared to Base 1) | | 6 (0) | 5 (0) | 2 (0) |
| Shift: Non to Mir (compared to Base 1) | | 1 (0) | 0 (0) | 1 (0) |

Base 1=initial baseline condition, Base 2=second baseline condition (block 4), Mir=mirror mode, Non=non-mirror mode, T=target, H=hand. Total error count reflects the cumulative error across 72-trial blocks for all participants combined.

them to employ a spatial translation to make an anatomical match in the non-mirror case (but not the mirror case). The severe slowing that occurred when such translations were encouraged leads us to question whether spatial translation is a natural and typical tendency in the non-mirror mode. Our results suggest that it is not, although subjects can apply that strategy if instructed to. Experiment 4 reinforces some of the conclusions reached from the earlier experiments. For one, subjects can flexibly adapt their behavior, based on the task and situation. As in Experiment 1, when stimulus markers were present on anatomically matching hands (or on corresponding targets), some subjects chose to imitate in the non-mirror mode, even though the mirror mode has been demonstrated to be most typical in imitation. When the markers were removed, a number of subjects switched back to the mirror mode, again reinforcing the conclusion that these switches in mode are flexible and adaptable to the task and situation.

The present findings are novel and theoretically important, primarily because they suggest that mirror and non-mirror modes of imitation are clearly distinct, the two modes obey different principles, and although people are clearly capable of imitating in either mode, one mode might be adopted over the other depending on the task and situation. Clearly, flexible adaptations to the task and situation can occur.

These findings which clearly point to differences in mirror and non-mirror imitation, might raise some challenges for present mirror neuron accounts. Based on functional neuroimaging in adults, bilateral inferior frontal and right posterior parietal areas are among those areas that are more active with mirror compared to non-mirror imitation (Koski et al., 2003). Not surprisingly, the areas more active during mirror imitation overlap with those that have been found to contain mirror neurons that respond to both observation and execution (Koski et al., 2002; Decety et al., 2002). Moreover, those areas map nicely onto the same neural regions found to contain mirror neurons in earlier studies on monkeys. It has been suggested by other researchers that mirror neurons provide the mechanism for direct matching between perception (observation) and action (execution). However, the present findings might suggest that a direct matching model might not always apply, or might apply in an attenuated manner, in the non-mirror mode. These issues lead to important questions such as: Is the same mirror neuron system used for both goal-directed and means-directed behavior in humans, and if so, is it activated to a different extent in the two cases? Or, are there specific subsystems of the mirror neuron system that operate depending on different constraints related to the task, situation, and response mode? What other systems might operate to inform and perhaps modulate regulation of the mirror system(s)? In our view, other systems might detect specific task and situational constraints (such as the presence of salient stimulus information), and then inform the mirror system(s) to attenuate their activation or yield to different (competing) response tendencies. In a recent review, we have suggested that the implementation of competitive processes which allow certain response tendencies to become activated while others are inhibited, depends on the basal ganglia (Franz, 2006). It seems possible that subcortical processes of this type also modulate activity of cortical mirror neuron systems.

However, rigorous experimental investigation would be required to test this possibility.

Perhaps a practical lesson can also be gained from these findings, particularly with respect to people who teach imitative skills to others (e.g., dancing, sport skills, tying shoes, weaving). Specifically, it seems important to be mindful of the possibility that there exist (at least) two competing modes of imitative behavior (mirror and non-mirror). Thus, if the model/teacher desires to teach a complex skill through imitation, she might consider providing stimulus cues to facilitate learning in the non-mirror case (e.g., wear a distinctive color cue on one hand, and instruct the students to wear the same distinctive color cue).

In summary, the present findings point to different modes of imitation as implicating different principles of performance. We suggest that these findings raise pertinent questions that must be answered about the way the brain and its mirror neuron system(s) operate in the different modes of imitation.

4. Experimental procedures

4.1. Experimental procedure 1

4.1.1. Apparatus

The basic experimental setup is shown in Fig. 3. Panel A is a picture of the setup with participant, model, and computer. The computer screen can be seen only by the model, and the participant sits facing the model. Panel B is a close-up of the computer screen diagrams shown to the model for each type of trial. Each diagram shows an arrow from the home key to the target so that the model easily knows what movement to make. Panel C is an overhead view of the desk with the templates viewed by the participant and model. Each set of four dots consists of two home positions located closest to each participant (one for each hand) and two targets that are 20 cm away. The template condition that is shown is the right target marked condition. No markers were shown for the baseline condition, and markers were on the hands (rather than on the targets) for the hand-marked conditions.

A Nest of Birds (Ascension Technology), with four 8 mm sensors was used to provide position data of both hands of the participant and both hands of the model throughout the testing session. The Nest of Birds uses magnetic tracking technology to accurately track the four sensors simultaneously (at 70 Hz). Using a direct interface into a PC computer, the Nest of Birds was run using an in-house collection program written in Matlab. A threshold of 10% peak velocity (computed off-line on an individual trial basis) was used to determine movement onset. Specifically, movement onset was determined when the velocity exceeded this threshold and after three consecutive positive acceleration points took place within 60 ms. Using in-house built interactive interfaces, we visually compared the trajectories of all sensors with the movement onset threshold determined using our algorithm to be sure it was working correctly. Spatial resolution was 0.25 mm. Movement offset was determined as the time at which the sensor remained within a spatial area of 0.50 mm for at least 3 consecutive samples.

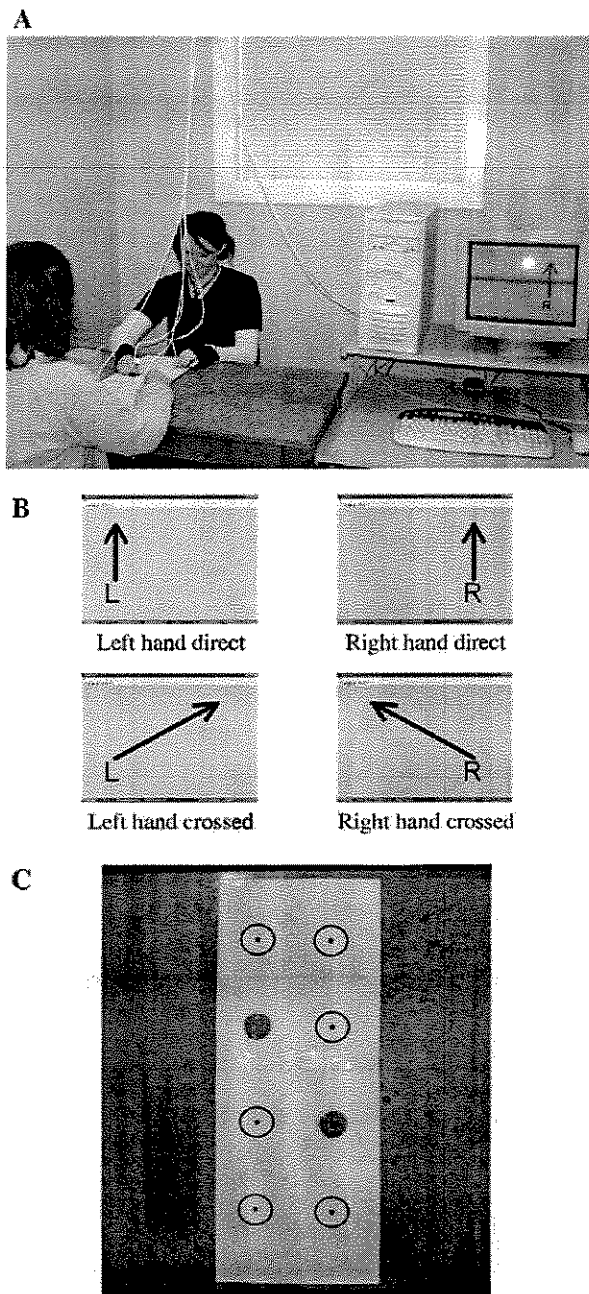


Fig. 3 – Schematic of the apparatus and setup for all experiments (A), the four possible diagrams that the model sees to instruct her what movement to produce on each trial (B), and an example of the templates shown in the right target marked condition (C). See text for details.

4.1.2. Participants

There were 20 participants (half males), with a mean age of 23.4 years. Handedness assessments indicated that they were all right-handed ($MN = .81$, where -1.0 indicates strongly left-handed, and 1.0 indicates strongly right-handed: Oldfield, 1971). None had any known neurological or movement disorders, and all had normal or corrected vision.

4.1.3. Stimuli

The apparatus displayed in Fig. 3A was used in all experiments described herein. In experiments involving stimulus markers, a red circular marker (diameter = 4 cm) was placed either on one hand of the model and participant, or one target of the model or participant (e.g., Fig. 3C), depending on experimental condition. On the hand marked conditions, the marker was placed on the knuckle of the middle finger so that it was visually salient to both model and participant. The markers were always anatomically matching, because our aim was to determine whether the typical mirror-mode advantage would reverse, producing a non-mirror mode advantage, under these conditions.

4.1.4. Design

Subjects were divided into two groups by odd-even split. The only difference in testing was that one group was always instructed to imitate the model using mirror-image movements (specular), as though looking in a mirror. For the other group, participants were instructed to move the same hand (anatomical) as the model moved, and if the model moved to the target on her right (left), participants should also move to the target on their right (left). From here on, we will use the abbreviations Mir to denote the mirror (specular) mode (group), and Non to denote the non-mirror (anatomical) mode (group) for simplicity.

Each participant performed three conditions, all counter-balanced: baseline, hand marked, and target marked. The baseline involved no stimulus markers. For the hand marked condition, one red marker was placed on either the right hand of both the model and participant, or on the left hand of the model and participant. Similarly, for the target marked condition, one red marker was placed on the target directly in front of the model's right (left) hand and directly in front of the participant's right (left) hand. In each case, the hand/target that was marked was counterbalanced across participants within each group so that either the left hand/target or the right hand/target was marked, with the constraint that the marked hand (or target) always matched anatomically for the participant and the model. Note, however, that within a block of trials, either the hand or the target (but never both) was marked (and there were no markers in baselines).

We did not instruct participants in either group to attend to the markers. Rather, both groups were simply instructed to imitate the model in either the mirror mode (Mir group) or the non-mirror mode (Non group) as quickly and accurately as possible after the model completed her movement. The same model was used across all experiments contained herein.

4.1.5. Procedures

Each of 3 blocks (baseline, hand marked, target marked) was tested for each participant in counterbalanced order. Each condition consisted of 72 trials in which the movement on any trial was completely unpredictable (1 of 4 possibilities: 2 hands \times 2 targets). Prior to the experimental blocks, each participant was talked through a few practice trials in the Mir or Non mode (depending on assignment). Sensors were held between the thumb and index finger of each hand of both the participant and the model. When ready, the model and experimenter calibrated the sensors by placing them first on

the home keys and waiting 2 s while the computer collected the sample points, and then on the target keys, again while waiting 2 s for computer collection. Provided there was no movement during the 2 s on each placement, and the sensors were within a 2 mm radius of the center of each home key/target region, the calibration was successful (to a spatial precision of 0.25 mm). Calibration was repeated if unsuccessful the first time, and no more than two attempts were ever necessary. After calibration, the experimental session began, with the computer displaying a movement in simple diagrammatic form to the model who then produced the movement (see Fig. 3B), and the participant was to follow by imitating that movement. Thus, each trial began with the computer display of the trial, and the display remained on the screen until the model began her movement. The computer then recorded position data of all four sensors. Upon termination of the participant's movement, a 2-s inter-trial interval occurred before the next stimulus display was presented by the computer in full vision of the model.

4.1.6. *Dependent measures of interest*

Performance errors were recorded automatically as errors of hand-selection, target-selection, or both hand and target selection. These were tallied for analyses. Accuracy of hitting the target was computed as the deviation in the X and Y dimension from the target center (however, we will not be reporting these latter effects because they were uninformative, and all subjects landed within the target regions on correct trials). Of primary interest was the measure of reaction time (RT), computed as the hand movement onset time of the participant (relative to hand movement onset of the model). Note that we also computed RT of the participant relative to movement offset of the model and the pattern of effects was virtually identical to those we report for RT. Movement time (MT) and average velocity were also measured to ascertain whether the two different modes of imitation produced marked differences. We expected that our manipulations would reflect primarily the planning properties rather than movement-related properties, so our expectation was that our manipulations would primarily influence RT. MT was computed from the end of the RT interval to the termination of movement. Movement velocity was computed as the first derivative of position data, based on the X–Y position data (the Z dimension was regarded as negligible because movements were only slightly above the table surface). Although all variables were collected both for the participants (who performed the imitation task) and the model, we report only those for participants.

4.2. *Experimental procedure 2*

4.2.1. *Participants*

A naive group of 20 participants was recruited from student job search in exchange for \$10. Half were males. They were all right-handed (mean handedness score = 0.76: Oldfield, 1971).

4.2.2. *Apparatus, design, procedures*

The apparatus was identical to that used in Experiment 1 (Figs. 3A, B). The only substantial change was that rather than manipulating the presence or absence of markers and running a completely random (unpredictable) series of trials within

each block (as in Experiment 1), we manipulated predictability of the hand and/or target. Each participant performed each of 6 experimental conditions (in separate blocks) in random order. In two blocks, the hand used to move was always the same (hand certain: left or right), but the target (left or right) varied randomly. In two other blocks, the target of the movement was always the same (left or right), but the movement hand varied randomly. On the remaining blocks, the hands and targets were completely uncertain, or the hand and targets were completely certain. The former of these two controls (all uncertain) was identical to the baseline condition of Experiment 1 (except now it was among 6 conditions rather than only 3). The 'all certain' condition involved the identical hand and target (and therefore identical movement) on every trial of the block. Because there were four possibilities for this condition, each possibility was quasi-counterbalanced across participants in the attempt to have equal numbers of subjects performing each combination of specified hand and target. Note, however, that these manipulations were not explicitly indicated to participants. Participants were instructed only to perform the movements in the Mir or Non modes (as in Experiment 1), with half the participants in each of the two instruction conditions. After data collection, 2 participants from each group (Mir and Non) were eliminated due to too many errors (>40% for each). In all four of these participants, there were severe hesitations in movement, and a number of trials in which one target was first touched and then the other one was touched, as though participants were attempting to correct performance online. This reduced our analyzable sample to 16. As a result, we also eliminated the 'all certain' condition from analysis because now the unique combinations of hand and target in that condition were not close to being equally represented (and note that the 'all certain' condition was not of interest to our hypotheses). We analyzed the remaining conditions after collapsing across the left and right hand (or target) conditions because there were no significant differences between them. The conditions were therefore (1) baseline: all uncertain, (2) hand certain (target uncertain), and (3) target certain (hand uncertain).

4.3. *Experimental procedure 3*

For the hand-marked conditions, we placed a green dot on one hand and a red dot on the other hand of the model, and placed corresponding colored dots on the participant's hands. For the target-marked conditions, we placed the red and green dots on the model's set of targets and on corresponding targets of the participant (again with color congruence for left targets and for right targets). All subjects in the Non group were then shown by an experimenter that color congruence would be very obvious if the participant was rotated 180°, and this type of translation of viewer perspective was encouraged. No demonstration was given to the Mir group.

This experiment had 3 conditions randomized: baseline, hands marked, and targets marked. There were 24 new participants, with half of them randomly assigned to the Mir group and half randomly assigned to the Non group. Participants were explicitly instructed to imitate on the basis of this assignment, with either mirror imitation (Mir) or non-mirror imitation (Non). The three conditions were randomly

administered. In addition, the Non group was shown the spatial translation demonstration just prior to performance of the task. To ascertain what strategy was consciously used by participants, we later queried them. In all other respects, the methods were similar to those of Experiment 1.

4.4. Experimental procedure 4

In the previous experiments, conditions were counterbalanced. Thus, approximately 1/3 of participants in Experiment 1 produced the baseline control prior to either of the stimulus marked conditions. In Experiment 2, given there were 6 conditions, only 1/6 of participants performed the baseline condition first. Due to statistical power, it was not possible to find reliable effects of task order, particularly with respect to whether the baseline condition was performed prior to the stimulus marker conditions of Experiment 1 or the certainty conditions of Experiment 2. Nor was it possible to examine whether previous exposure to other conditions resulted in measurable effects on performance in a baseline condition performed subsequently. To examine these issues, in Experiment 4 we included a baseline condition as the initial condition for each participant, and a second baseline condition as the last condition for each participant. The two intervening conditions were the target marked and hand marked conditions (as in Experiment 1), counterbalanced across participants. Note, as indicated above, participants were not explicitly instructed in this experiment to perform in the mirror or non-mirror mode. Rather, they were instructed to imitate the experimenter in the manner most natural. Because the marker present conditions facilitated performance of the Non group in Experiment 1, we predicted that people might shift from mirror imitation in the initial baseline condition to non-mirror imitation in the marker conditions if performance depends largely on stimulus information associated with the hands or targets (stimulus-based account). We further predicted that subjects would shift back to the mirror mode in the second baseline condition when markers were again not present. On the other hand, if a particular mode of imitation, once learned, tends to be used persistently, then we would expect to find that participants who begin in one mode would continue imitating in that mode, regardless of changes in stimulus information (experience-based account). Twenty participants of approximately the same demographic characteristics as in other experiments were recruited for participation.

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