RESEARCH NOTE

Stimulus-driven selection of routes to imitation

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Abstract Several models have proposed that an action can be imitated via one of two routes: a direct visuospatial route, which can in principle mediate imitation of both meaningful (MF) and meaningless (ML) actions, and an indirect semantic route, which can be used only for MF actions. The present study investigated whether selection between the direct and indirect routes is strategic or stimulus driven. Tessari and Rumiati (J Exp Psychol Hum Percept Perform 30:1107–1116, 2004) have previously shown, using accuracy measures, that imitation of MF actions is superior to imitation of ML actions when the two action types are presented in separate blocks, and that the advantage of MF over ML items is smaller or absent when they are presented in mixed blocks. We first replicated this finding using an automated reaction time (RT), as well as accuracy, measure. We then examined imitation of MF and ML actions in the mixed condition as a function of the action type presented in the previous trial and in relation to the number of previous test trials. These analyses showed that (1) for both action types, performance was worse immediately after ML than MF trials, and (2) even at the beginning of the mixed condition, responding to MF actions was no better than responding to ML items. These results suggest that the properties of the action stimulus play a substantial role in determining whether imitation is mediated by the direct or the indirect route, and that effects of block composition on imitation need not be generated through strategic switching between routes.

Introduction

It has been proposed that action imitation can be accomplished via two routes (e.g. Rothi et al. 1991; Rumiati and Tessari 2002; Tessari and Rumiati 2004). This theory proposes that unfamiliar or ML actions are imitated by mapping an observed action directly onto an executed action, according to its visuospatial properties. In principle, familiar or MF actions can also be imitated via this direct visuospatial route, but in addition, they can be imitated via an indirect semantic route. This semantic route involves an additional stage of processing; between visual analysis and preparation of motor output, a semantic representation of the action is retrieved from long-term memory. Neuroimaging and neuropsychological research have provided support for the existence of two routes of imitation (Decety et al. 1997; Rumiati et al. 2005; Tessari et al. 2007).

However, in a behavioural study with neurologically healthy participants, Tessari and Rumiati (2004) found evidence suggesting that MF and ML actions are not always imitated via distinct routes. Imitation of ML actions was less accurate than imitation of MF actions when the two action types were presented in separate blocks (blocked condition), but there was no detectable difference in the accuracy of imitating MF and ML actions when they were presented in random order within the same blocks (mixed condition). Similar results were obtained when testing patients with apraxia (Tessari et al. 2007). On the basis of these findings, Tessari and Rumiati (2004) proposed that ML actions must always be imitated via the direct route, because ML actions are not represented in

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semantic long-term memory, but the route for imitation of MF actions can be selected strategically, according to which is likely to be more efficient. The indirect route places fewer demands on working memory than the direct route because semantic long-term memory represents each action as a unit, whereas the direct route requires that the action be decomposed into chunks that are each held in working memory. Therefore, the direct route will be selected when MF actions are presented in the blocked condition. However, in the mixed condition, use of distinct routes for the two action types incurs switch costs, and these switch costs outweigh the advantages of using the indirect route for MF actions. Therefore, in the mixed condition, it is more efficient to select the direct route for both action types. Given that participants were not instructed about the composition of the block, Rumiati et al. (2005) proposed that, in the mixed condition, participants switched between routes for a few trials, discovered from this experience that switching was inefficient, and then strategically selected the direct route for use in all the remaining trials.

Thus, the lack of an observable performance difference between imitation of MF and ML actions under mixed conditions may be due to strategic selection of the direct route for both action types. However, this pattern of results is also compatible with stimulus-driven route selection, which suggests that when each action is observed both routes initially compete for selection. When an action is recognised as familiar or MF, the indirect route is automatically activated. If not, the direct route is used. This alternative hypothesis implies that, even under mixed conditions, imitation of MF actions is mediated by the indirect route and imitation of ML items is mediated by the direct route. However, the advantage of MF over ML items is reduced under mixed conditions because processing of a ML item, via the direct route, makes heavy demands on working memory, and thereby interferes with processing of any item that follows it in the list. When presentation is blocked, this carry-over cost is borne solely by other ML items, enhancing the advantage of MF over ML items. However, when MF and ML items are presented in random order, the carry-over cost affects the imitation of ML actions in half of the trials, and of MF actions in half of the trials. Therefore, it erodes the advantage of MF over ML items.

The present study examined the effects of block composition (blocked versus mixed) on the imitation of MF and ML actions in a sample of neurologically healthy participants, and sought to distinguish the strategic selection and stimulus selection hypotheses by analysing performance for MF and ML action types in the mixed condition according to (1) whether an action item was preceded by a MF or a ML action, (2) whether an action

item was MF or ML itself, and (3) the stage of testing in the mixed condition. Because there is a risk of ceiling effects when imitation accuracy is measured in neurologically healthy participants, to enhance measurement sensitivity, we used an RT index of imitative performance in addition to an accuracy measure. The strategic selection and stimulus selection hypotheses both predict that imitation of MF actions will be superior to imitation of ML actions in blocked conditions, and that this advantage for MF actions will be greater than that in mixed conditions. However, the hypotheses make different predictions about the pattern of data in the mixed condition. First, the stimulus selection hypothesis predicts superior imitation when either MF or ML actions are preceded by a MF action rather than a ML action. In contrast, the strategic selection hypothesis predicts no difference according to the action type that precedes an action, because all actions are imitated via the direct route. Second, the strategic selection hypothesis predicts no difference in imitation of actions which are MF and ML themselves, because both action types are imitated via the same route. The stimulus selection hypothesis predicts that imitation of MF actions will be superior to imitation of ML actions, despite a smaller difference compared with blocked conditions, because MF actions are processed by the less demanding indirect route. This difference may not have been observed in previous studies if the measures of imitative performance were not highly sensitive. Third, the strategic selection hypothesis predicts that imitation of MF items will be superior to imitation of ML items early in testing under mixed conditions, during the period when participants are switching between routes and learning that this is not efficient, and subsequent loss of this advantage when they resort to using the direct route for both action types. In contrast, the stimulus selection hypothesis predicts no such change in the course of mixed blocks, because it assumes that distinct routes are used throughout for the imitation of MF and ML actions.

Method

Twenty-four consenting, healthy volunteers with an average age of 21.9 years, 10 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. The study was approved by the University College London ethics committee, and performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Participants were tested individually in a well lit room. They were required to stand approximately 1.5 m away

from a computer screen (75 Hz, 400 mm, 96 DPI), and to hold down a large response button (9.5 cm diameter) with their right hand. The button was positioned at hip height and approximately 20 cm in front of the participant's body. They were instructed to release the response button in order to imitate actions observed on the computer screen with their right hand, and to ensure that they returned their hand to the button before a beep sounded, signalling the onset of the next trial. They were told that they must execute the action as soon as they had released the button, they were told not to pause after button release, and they were observed throughout the experiment to ensure that they obeyed these instructions.

Each imperative stimulus was a hand and arm action performed by a male model with his left hand. The stimulus display subtended approximately 8.9° of visual angle horizontally and 6.6° vertically. There were 20 pantomimes of MF actions and 20 ML actions, and the ML actions were constructed by performing MF actions with a different spatial relationship between the hand and arm, and the trunk (see "Appendix"). The videos were those used by Tessari and Rumiati (2004). The stimulus actions were performed with the model's left hand, therefore, executed actions matched the observed actions spatially, but not anatomically.

There were four blocks: one block contained only MF actions (blocked MF), one block contained only ML actions (blocked ML), and two blocks contained MF and ML actions (mixed). Whether participants undertook the blocked or mixed condition first was counterbalanced, as was the order of blocked MF and blocked ML conditions. All trials began with presentation of the stimulus action, which was of 1,500 ms duration. This was followed by a black screen, which was accompanied 1,000 ms later by a beep of 250 ms duration, after which the next stimulus action was presented. Each block presented, in random order, 80 stimulus trials. In the blocked condition, a block comprised four repetitions of each of 20 action stimuli. In the mixed condition, a block comprised two repetitions of each of 40 action stimuli. Before testing commenced, participants completed 12 practice trials including 6 MF actions and 6 ML actions. These actions were not presented in the test blocks.

In addition to RTs, the executed actions were scored for similarity to the observed actions on a 5-point scale. An action rated as '1' bore no similarity at all to the observed action, i.e., the spatial trajectory of the hand and arm matched the observed action no more than any of the other actions in the stimulus set. An action rated as '5' was a perfect match, i.e., the positions and trajectories of the participant's hand and arm were indistinguishable from those of the model. Scores of 2, 3, and 4, were given to actions which fell between these levels of similarity, with

approximately equal intervals between each of the points on the scale. The scorer was naïve to the hypotheses and predictions under investigation.

Results

Mean RT to imitate MF and ML actions, in the blocked and mixed conditions, was calculated for each participant. Trials rated as '1' for similarity (0.7%), RTs under 150 ms (3.2%), and trials in which participants had not returned their hand to the button before the start of the trial (5.7%), were excluded from the RT analysis.

The RT data (Fig. 1a, columns) were subjected to ANOVA in which the block type (blocked versus mixed) and action type (MF versus ML) were within-subjects variables. This analysis indicated a block type × action type interaction [$F(1,23) = 10.2$, $P < 0.005$]. Simple effects analyses indicated faster RTs to imitate MF than ML actions in the blocked condition [$F(1,23) = 7.6$, $P < 0.02$], but not in the mixed condition [$F(1,23) = 2.5$, $P = 0.1$]. Analysis of the similarity data (Fig. 1a, lines) indicated that MF actions were imitated more accurately than ML actions in blocked [$F(1,23) = 20.0$, $P < 0.001$] and mixed conditions [$F(1,23) = 21.6$, $P < 0.001$], but there was a lesser advantage of MF over ML items in the mixed condition (block type × action type: $F(1,23) = 5.8$, $P < 0.03$).

To investigate the source of this interaction effect, the data from the mixed condition were subjected to further analysis. The first of these further analyses examined RTs to MF and ML action items as a function of whether each was immediately preceded by a MF or a ML item. The results, shown in Fig. 1b (columns), were subjected to ANOVA in which the action type of the present trial (MF versus ML) and the action type of the previous trial (MF versus ML) were within-subjects variables. A main effect of action type in the preceding trial [$F(1,23) = 4.9$, $P < 0.04$] indicated that responding was slower when the item was preceded by a ML rather than a MF trial. No other main effects or interactions were significant. This effect of action type in the preceding trial could not have been due to a speed-accuracy trade-off because inspection of the similarity data (Fig. 1b, lines) indicated that imitation was not only faster but also more accurate, when the preceding trial involved a MF rather than a ML item [$F(1,23) = 3.0$, $P < 0.05$, one tailed].

In the final analysis, the RT data from the mixed condition were divided into 16 successive bins of 10 trials each (Fig. 1c, columns), and subjected to ANOVA in which the bin (1–16) and action type (MF versus ML) were within-subjects variables. (The data from two participants had to be excluded from the RT analysis because they did not
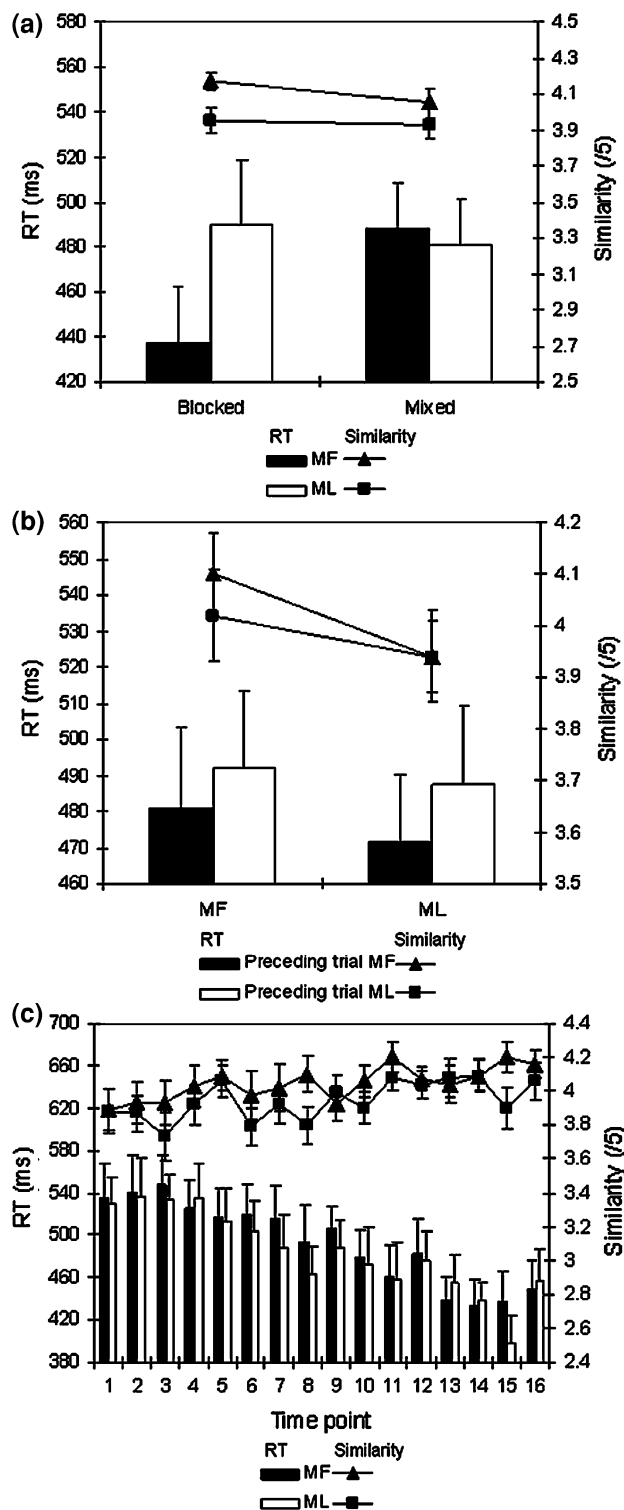
Fig. 1 Mean RT, and mean similarity of executed actions to observed actions: **a** when imitating MF (*shaded bars*, *triangles*) and ML (*open bars*, *squares*) actions presented in the blocked and mixed conditions, **b** when imitating MF and ML actions in the mixed condition, when the preceding action was MF (*shaded bars*, *triangles*) and ML (*open bars*, *squares*), and **c** when imitating MF (*shaded bars*, *triangles*) and ML (*open bars*, *squares*) actions, at 16 successive bins during the mixed condition. *Vertical bars* indicate the standard error of the mean

contribute data to every one of the 32 cells of the analysis.) This analysis, and a parallel analysis applied to the similarity data (Fig. 1c, lines), produced main effects of bin [RT: $F(15,315) = 5.1$, $P < 0.001$, similarity: $F(15,345) = 2.5$, $P < 0.02$, Greenhouse Geisser corrected], indicative of faster and more accurate responding when participants were more practised at the task, but did not produce a significant interaction between bin and action type (both Fs < 1.2). Thus, there was no evidence of a greater difference between MF and ML trials in the early mixed trials compared with later mixed trials.

Discussion

The present study sought to replicate a previously reported effect of block composition on the imitation of MF and ML actions (Tessari and Rumiati 2004) and investigated the roles of stimulus driven and strategic processes in selecting between direct visuospatial, and indirect semantic, routes to imitation. Replicating the previously reported effect, we found that the superiority of imitation of MF actions, relative to ML actions, was greater under blocked than mixed conditions. The fact that this pattern of results was obtained with an RT measure of imitative performance, as well as with an accuracy measure, as in previous studies, suggests that the effect is robust, and therefore that its investigation is likely to provide important insights into the processes mediating imitation.

As predicted by the stimulus selection hypothesis, the present study found that, in the mixed condition, actions were imitated faster and more accurately when they followed a MF, rather than ML, action. This finding is consistent with the stimulus selection hypothesis because it assumes that processing of ML items via the direct route depletes working memory resources, relative to processing of MF items via the indirect route, and thereby has a detrimental effect on performance in any subsequent trial. This finding is less consistent with the strategic selection hypothesis; if MF and ML actions are both imitated via the direct route, they should place equal demands on working memory, and there should be no effect of the preceding action type on imitation of the present action. We also failed to find any evidence of strategic change in the course of testing in the mixed condition; the difference between RTs and accuracy for MF and ML items did not change systematically throughout the mixed blocks. This is consistent with the stimulus selection hypothesis, which takes action stimulus types to determine the route of imitation, and these do not change during the block. It is less consistent with the strategic selection hypothesis, which suggests that participants use the indirect route to imitate MF actions at the beginning of the mixed condition, and

therefore perform better on MF than on ML trials at this stage, and that participants subsequently adopt the direct route for both the MF and ML items, resulting in equivalent performance for the two action types later in the test period (Rumiati et al. 2005).

If stimulus features are solely responsible for selection between direct and indirect routes, it was also predicted that the advantage of MF over ML actions would be smaller in mixed than in blocked conditions, but still present when items are mixed. Several previous experiments show a trend in this direction (Tessari and Rumiati 2004, Experiments 2B and 3A; Tessari et al. 2006; Toraldo et al. 2001; De Renzi et al. 1980). In the present study, there was no difference in RT to MF and ML actions in the mixed condition, but MF actions were imitated more accurately than ML actions. Thus, the absence of any effect of action type on RT in the mixed condition of the present experiment may have been due to a speed-accuracy trade-off. It is likely that a speed-accuracy trade-off accounts for the lack of effect of action type on RT, because the pattern of data in this experiment is much more consistent with the stimulus selection hypothesis than the strategic selection hypothesis. Specifically, there were three effects in the mixed condition on which the hypotheses made different predictions: (1) preceding action type, (2) present action type, and (3) stage of testing. Of these effects, the RT and accuracy data for (1) and (3), and the similarity data for (2), namely 5/6 of the effects, support the stimulus selection hypothesis over the strategic selection hypothesis.

Whether route selection is driven solely by stimulus features or by a combination of stimulus features and strategic processing, many questions remain about the neural bases, developmental origins, and differential functions of the direct and indirect routes. Using PET, Decety et al. (1997) found that MF actions are imitated via left frontal and temporal regions, and that ML actions are imitated via right parietal-occipital areas. If, as the stimulus selection hypothesis suggests, MF actions are consistently processed via the indirect route and ML items via the direct route, this study provides information about the neural mechanisms on which the two routes depend.

Regarding the developmental origins of the two routes, the associative sequence learning model (ASL) suggests that experience plays a crucial role (e.g. Heyes 2001; Heyes and Ray 2000). According to this model, the direct route acquires its capacity to match visual with motor representations of action components from experience in which such components were simultaneously observed and executed (e.g. Heyes et al. 2005; Catmur et al. 2007; Press et al. 2007; Vogt and Thomaschke 2007). The indirect route develops through acquired equivalence (Hall 1991); experience in which a 'bridging stimulus', such as the sound of a word, is paired with observation and execution of an action. The bridging stimulus may be paired on some occasions with action observation, and on other occasions with action execution, or these pairings may occur at the same time, when simultaneously observing and executing action in the presence of the bridging stimulus. This experience-based account is consistent with the finding that ML actions are imitated more accurately following practice with the ML items (Tessari et al. 2006). However, it raises important questions about the precise nature of the functional specialisation of the two routes to imitation. For example, is the indirect route specialised for MF actions per se, or for actions that are highly familiar, or highly 'nameable' as wholes? These questions are priorities for future research.

In conclusion, the present study confirmed, using an RT and accuracy measure, that imitation of MF actions is superior to that of ML actions when the two action types are presented in blocks, and that this difference is smaller or absent when they are mixed. This provides support for the view that there are two neurologically and functionally distinct routes to imitation, a direct visuospatial route and an indirect semantic route. However, the results of the present study cast doubt on the assumption that the direct and indirect routes can be strategically deployed; they suggest that these routes are automatically activated by properties of the action stimulus.

Appendix

There were 20 pantomimes of MF actions and 20 ML actions, and the ML actions were constructed by performing MF actions with a different spatial relationship between the hand and arm, and the trunk. For example, the MF action of drinking consisted of bringing the hand from the front of the torso to the mouth, with the hand in a 'C' formation, at first in the horizontal plane, and then rotating to the vertical plane. The ML version consisted of bringing the hand to the forehead rather than the mouth, but all other components of the action were identical. The videos were those used by Tessari and Rumiati (2004).

MF actions

1. To clean with a cloth
2. To comb
3. To paint (a wall)
4. To iron

5. To shave
6. To drink
7. To eat with a fork
8. To put on lipstick
9. To pour with a bottle
10. To brush one's own teeth
11. To stir
12. To hammer
13. To play tennis
14. To write
15. To strike a match
16. To saw
17. To cut with a knife
18. To screw in a lightbulb
19. To use a key
20. To smoke.

ML actions

1. To clean with a cloth: cleaning performed at 90° from where it is normally performed
2. To comb: combing action performed on the face from top to bottom
3. To paint: painting action performed along the main axis of body (from chest to hip)
4. To iron: ironing movement performed diagonally in front of the body
5. To shave: shaving movement performed on the chest, from bottom to top
6. To drink: drinking movement performed with the hand moving to the forehead instead of the mouth
7. To eat: eating movement performed with the hand moving to the shoulder instead of the mouth
8. To put on lipstick: drawing a circle on the chest
9. To pour: pouring movement done in reverse
10. To brush teeth: brushing movement on the shoulder
11. To stir: stirring movement performed horizontally on the left side, away from the body
12. To hammer: hammering movement performed with the hand 90° from the body midline
13. To play tennis: reverse swing movement, starting from the upper-left shoulder
14. To write: writing movement above the head
15. To strike a match: striking movement along the left lower arm
16. To saw: sawing movement performed at 90° from the normal position, across the front of the body
17. To cut with a knife: cutting movement performed in reverse and on the right side of the body

18. To screw in a lightbulb: movement of screwing in a lightbulb performed 90° in front of the body and toward the left side of the body
19. To use a key: turning a key at 90° from the normal position, with the key pointing up
20. To smoke: smoking movement toward the chest instead of the mouth.

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