Route switching in imitation: Should I stay or should I go?

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Abstract

The dual-route models of action imitation predict that, normally, known actions are imitated by using a semantic route - i.e. by activating a representation of the action from memory - whereas unknown, new actions are reproduced by using a direct route - i.e. by performing a visuo-motor transformation of the input into an output. Here we aimed at establishing the nature of the dominant process used by healthy adult individuals in imitation. Participants performed an imitation task with both predictable switches and pseudorandom, unpredictable switches The predictable switches are less cognitively demanding, and allow the voluntary selection of the most suitable process for performing the task; whereas the unpredictable switches are more demanding and lead to a more intense use of strategies. We observed significant switch costs only in the predictable switch condition, when subjects had to rely on working memory to keep track of the underlying sequence, but not in the pseudorandom sequences, where participants could select the direct route to decrease the cognitive effort. These findings suggest that the semantic route is the dominant, more automatic and less-demanding process for action imitation. The strategic selection of route in action imitation and in monitoring behaviour seems to be an adaptive acquisition.

Keywords: imitation, cognitive strategies, meaningful and meaningless actions, switching cost.

Introduction

Since Meltzoff and Moore (1977; 1983; 1989) discovered that infants can imitate facial expressions and hand gestures within a few hours of life, it has been widely accepted that imitation is an innate human ability. Many studies in both the context of social psychology (e.g. Dijksterhuis & Bargh 2001; Lakin et al. 2003) and cognitive neuroscience (e.g., Brass et al. 2000; Brass et al., 2005; Lhermitte et al. 1986; De Renzi et al. 1996) have suggested that imitation is a contagious and automatic process. Brass and colleagues (Brass et al. 2001; Brass et al. 2000), for example, showed that movement observation influences movement execution in a task in which the response is not related (i.e., a simple stimulus-response compatibility paradigm with finger movements), thus supporting an automatic tendency to imitate also in adults. Some authors have also shown that patients with frontal lesions suffer from imitation behaviour (Lhermitte et al. 1986; De Renzi et al. 1996) and they imitate the examiner's movements even if instructed not to do so. It has been proposed that the deficit is caused by a lack of inhibition of the mediobasal frontal cortex on the parietal lobe. This effect is not to a general effect that involved overlearned skills but it is specific for inhibiting actions (Brass Derrfuss and von Cramon, 2005).

In contrast, patients with ideomotor apraxia exhibit a dramatic reduction of their ability to imitate actions, and often to pantomime on verbal command and visually presented objects (De Renzi et al. 1980), in particular after lesions of the left inferior posterior parietal cortex (e.g. Goldenberg and Hagmann 1997; Buxbaum et al. 2005; Tessari et al. 2007).

Models of imitation

Many cognitive models have been put forward in order to explain imitative behaviours in humans. They range along a continuum. On the one end there is the direct matching approach (Prinz 1997; Hommel, Müsseler, Aschrsleben and Prinz 2001), stating that observing the effect of an action facilitates its execution because perception and action planning share a common representational code. In the middle, the Active Intermodal Mapping (Meltzoff & Moore 1977; 1997), suggesting that imitation is a matching-to-target process, based on the proprioceptive feedback loop that allows infants' motor performance to be evaluated against the perceived target. On the other end of the continuum, there are theories that require more than a simple process. One such theory is the goal-directed theory (Bekkering, Wohlschläger and Gattis, 2000), according to which imitation is decomposition-reconstruction process dependent on sub-goals hierarchically organized (i.e. the objects to which the actions are directed, the agents that perform actions, or the movement) and on cognitive

resources available (Wohlschläger et al. 2003). Another such model is the one based on neuropsychological observations of patients with selective deficits for imitation of meaningless or meaningful actions (Goldenberg and Hagmann 1997; Peigneux et al. 2000; Bartolo et al. 2001; Tessari et al., 2007). According to this model, there are two processes for imitation: a direct route for reproducing novel actions (but also those already known) that can parse seen actions in subcomponents that the person is already able to perform, and a semantic, indirect route for reproducing only over-learned actions, that are already stored in long-term memory. Some of these models also include a specific temporary memory structure, common to both processes, for holding the gestures in memory until they are reproduced (Cubelli et al., 2000, who call it "buffer"; Rumiati & Tessari, 2002; Buxbaum, 2001). This short-term/working memory subsystem is also connected to the long-term memory system and allows us to learn new actions (Tessari et al., 2006). Other authors introduced in this scheme also a supramodal representation of the body, based on the observations of patients who failed to reproduce postures not only by themselves but also on a manikin (Goldenberg & Hagmann, 1997; but see also Buxbaum, 2001).

Some support to the existence of two separate processes is provided also by some imaging studies that investigated the cerebral correlates of the mechanisms involved in actual imitation. A Positron Emission Tomography (PET) performed by Peigneux et al.'s (2004) found that imitation of familiar actions was associated with activations in the left angular and middle frontal gyri, the right supramarginal gyrus and inferior parietal lobule; whereas imitation of novel, meaningless actions was associated with inferior and superior parietal lobes bilaterally. Rumiati et al. (2005) required participants to imitated meaningful and meaningless actions in a PET study using a parametric design. A significant positive correlation with the amount of meaningful actions was found in the left inferior temporal gyrus, and a significant positive correlation with the amount of meaningless movements was observed in the right parieto-occipital junction. Moreover, direct categorical comparisons showed increased neural activity in the left inferior temporal gyrus, the left parahippocampal gyrus, and the left angular gyrus when imitating meaningful relative to meaningless actions. In contrast, imitation of meaningless (relative to meaningful actions) revealed increased neural activity in the superior parietal cortex bilaterally, in the right parieto-occipital junction, in the right occipital-temporal junction, and in the left superior temporal gyrus. Similar areas were found to be damaged in a neuropsychological study (Tessari et al., 2007). In particular, the brain structures damaged in left-brain damage patients who are able to imitate meaningful actions better than meaningless actions overlapped in the superior temporal lobe and the ventral portion of the angular gyrus; and those lesioned in the right-brain damage patients overlapped in the basal ganglia. On the other hand, the patients who imitated meaningless better than meaningful actions had lesions involving the lateral

and dorsal portion of the hippocampus, extending to the bordering white matter, and the dorsal angular gyrus.

Does the cognitive system strategically switch between the two processes? Evidence form healthy individual and brain-damaged patients

Results with both healthy subjects (Tessari & Rumiati, 2004) and brain damaged patients (Tessari et al., 2007) demonstrated that the composition of the list of the to-be imitated actions, that is the percentage of meaningful and meaningless actions, induces a strategic use of the two routes when limited cognitive resources are available. In a previous study (Tessari and Rumiati 2004) we tested healthy individuals with a deadline technique, consisting of a fast presentation of the stimulus and a very limited time for the response. This paradigm temporally reduced the cognitive resources available for performing the task. They found that when meaningful and meaningless actions were presented in a mixed list, then subjects selected the direct route for reproducing both types of action in order to avoid the effort of switching routes. However, when meaningful and meaningless actions were presented in separate lists a dissociation of the routes was observed: the direct route is used for imitating meaningless actions and the semantic route is used for the meaningful actions, inducing to a better imitative performance on the latter kind of actions. Similar results were observed in a study with brain-damaged patients, whose cognitive resources are reduced by the brain lesion (Tessari et al., 2007). Both left- and right-brain damage were required to imitate the meaningful and meaningless actions which presented either in separated blocks or intermingled. At a group level, patients performed better in the blocked than in the mixed condition, irrespective of the side of the lesion. Moreover, at a single-case level, a classical double dissociation in imitation of meaningful and meaningless actions was evidenced in two patients (cases 19 and 31). This double dissociation supports a functional independency of the two routes.

Which is the dominant process?

Some studies suggest that the direct route might be dominant in children (Meltzoff & Moore, 1977; 1997). However, this mechanism might loose its importance as the child becomes an adult equipped with a large vocabulary of actions. Therefore, it is plausible that, once a large repertoire of actions is acquired, the direct route is inhibited and imitation performance relies mainly on the semantic route (Brass et al., 2001; Lhermitte, 1983; Lhermitte et al., 1986). In the present study we aimed at assessing this hypothesis. To establish which of the two processes is the dominant one in healthy individuals, we employed a switching paradigm in an action imitation task (Allport & Wylie, 1999; Meuter & Allport, 1998). The task-switching paradigm is commonly used to investigate processes of cognitive flexibility and adjustments in the cognitive system. (see Rogers & Monsell, 1995; Monsell, 2003 for a

review). On this paradigm, subjects perform at least two different cognitive tasks, each of which can be either indicated by a cue or derived from a fixed sequence (i.e., AABBAA). Studies that made used of this paradigm constantly showed costs when switching from one task to another relative to when the same task is repeated. This cost is attributed to the application of a new task set and the persisting activation of the recently performed one (Monsell, 2003).

This paradigm is thus suitable for establishing whether the two imitative routes can be easily switched and which of the two is dominant. The switching paradigm might further reveal whether the selection of one route over the other is driven only by bottom-up factors, i.e. the list composition (see Tessari & Rumiati, 2004) or whether top-down selection also takes place.

In this study we investigated the role of the composition of the list (context) in strategy selection in healthy individual. A group of participants was presented with a) fixed sequences of meaningful and meaningless actions and, therefore predictable switches, which forced subjects to monitor the sequence; b) random switches that occurred after three, five or seven trials of meaningful or meaningless actions. This was thought to reveal the influence of bottom-up factor such as list composition on the selection between the two routes for imitation.

Experiment 1
Predictable switches

In this experiment we aimed at reproducing a condition in which the cognitive system can predict and guide the selection of the most suitable process for action imitation: fixed sequences of meaningful and meaningless actions were shown and predictable switches (every 5 trials) were used.

Method

Participants. Nineteen right-handed individuals, all students of the University of Bologna (9 males, average age=22.84, SD=1.98) participated in the experiment. They all had either normal or corrected-to-normal vision. Their handedness was tested using the Edinburgh Inventory (Oldfield, 1971).

Stimuli. We used 15 familiar, meaningful actions (pantomimes of object use; i.e. to iron, to pour with a bottle, to screw a light bulb, to write with a pen, to use a toothbrush,) and 15 novel meaningless actions (obtained by modifying the relationship between hand/arm and trunk in the meaningful actions). They were chosen from an original set of 20 meaningful and 20 meaningless actions used in previous studies (Tessari & Rumiati, 2004; Rumiati et al., 2005; Tessari et al., 2006; Tessari et al., 2007): Five independent individuals rated the meaningfulness and

meaninglessness of the actions from this original set; those actions that received the best average scores on a scale from 1 (minimum) up to 5 (maximum) from the five raters were selected and then employed as experimental stimuli.

Design and procedure. Both meaningful and the meaningless actions were presented in a random order, five times each in a single block. The sequence of events was structured as follows: Each trial started with an action that lasted for 1264 ms, followed by a 1000 ms blank interval, at the end of which a beep was played for 250 ms (see Figure 1). Participants were required to imitate each action immediately after its presentation (i.e., during the blank interval); the next trial appeared immediately after. In the "fixed" condition, alternated sequences of 5 meaningful and 5 meaningless actions were presented. All 30 actions (15 meaningful and 15 meaningless) were presented randomly in 5 subsequent sub blocks for a total amount of 150 trials. The participants were informed about the composition of the list (i.e., fixed sequences or random sequences), and they were asked to imitate the actions with their right limb. The actor performed the actions with his left limb. Participants' performance was videotaped and later scored independently by two naïve raters (As there was no significant difference between the scores of the two raters in both experiments: all p < 0.05, an analysis on the mean scores is used in the results section). An imitated action was scored as incorrect when one of the following errors occurred: Spatial error of the hand, spatial error of the arm, semantic errors (i.e. prototypicalization, body part as a tool), visual (i.e. partial perseveration, global perseveration, lexicalization), omission, and unrecognizable gestures (see Tessari & Rumiati, 2004, for a detailed description).
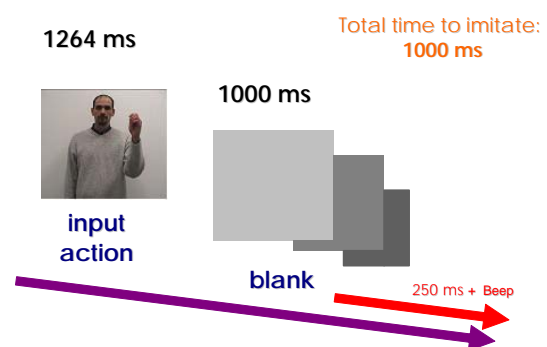

Figure 1: sequence of events into a trial

Results. A repeated measures analysis of variance (ANOVA) was performed only on the first and second trials, with Type of Action (meaningful vs. meaningless) and Order (first vs. second trial; this difference represent the switching costs) as within-subject factors, and imitation accuracy as dependent variable. Both Type of Action

(F(1,18)=0.07, p>.05) and Order (F(1,18)=0.15, p>.05) were not significant but their interaction was (F(1,18)=5.37, p<.05): a switching cost was found for the meaningful actions, with accuracy being lower for the first (mean=11.89, SD=1.45) than for the second (mean=12.37, SD=1.77) trial (paired-samples t-test: t(18)=1.84, p<.05). On the other hand, an opposite pattern emerged for the meaningless actions: accuracy on the first was better than on the second trial (mean=12.37, SD=1.89 and mean=11.74, SD=1.56, respectively; paired-samples t-test: t(18)=1.75, p<.05).
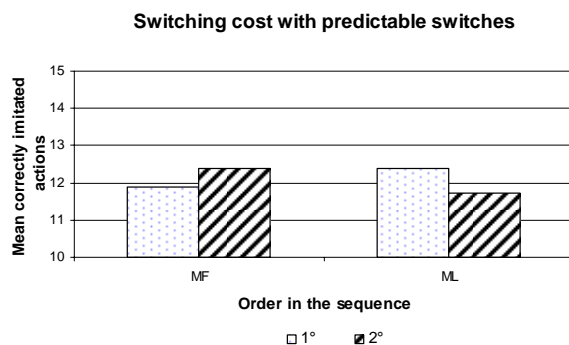
Switching cost with predictable switches

Figure 2: switching cost for meaningful (MF) and meaningless (ML) action in Experiment 1

Discussion. A significant switching cost (i.e. the average mean on a switch trial minus that on a repeat trial) emerged when imitating meaningful actions but not meaningless ones. According to Allport et al. (1994), the switch effect is greater when switching from a more difficult task to an easier one. Therefore, this cost seems to suggest that the semantic route, used for reproducing meaningful actions, is the most automatic process in adult individuals and need greater inhibition when switching to the direct route, that is necessary for imitating the meaningless actions. This was also suggested by results from imitation under time limits: despite the fact that when imitating without time constraints, no difference emerges between meaningful and meaningless action (see Experiment 1's introduction in Tessari & Rumiati, 2004), when time pressure is imposed and predictable switches (i.e. blocked presentation) are used, the human cognitive system is able to extract the regularity in the presentation sequence and to predict the forthcoming type of stimulus therefore applying the right process to perform the imitation task.

Experiment 2
Unpredictable switches

In this experiment, pseudorandom switches between meaningful and meaningless actions were used. This condition reproduces the mixed condition in Tessari and Rumiati (2004) where the direct route is usually preferred

for performing the imitation task in order to decrease cognitive effort of switching between the two processes. Under this condition we did not expect any switching cost.

Method

Participants. Twenty right-handed individuals, all students of the University of Bologna (11 males, average age=23, S.D.=2.22) participated in the experiment. They all had either normal or corrected-to-normal vision. Their handedness was tested using the Edinburgh Inventory (Oldfield, 1971).

Stimuli. We used the same stimuli as in Experiment 1.

Design and procedure. They were the same as in Experiment 1 with respect to the trial structure, but alternated sequences of randomly presented 3, 5 or 7 meaningful and 3, 5, 7 meaningless actions. This condition should simulate the mixed presentation in Tessari and Rumiati (2004). The participants were informed about the composition of the list (i.e., fixed sequences or random sequences), and they were asked to imitate the actions with their right limb.

Results. A repeated measures analysis of variance (ANOVA) was performed only on the first and second trials, with Type of Action (meaningful vs. meaningless) and Order (first vs. second trial; this difference represent the switching costs) as within-subject factors and imitation accuracy as dependent variables. Both Type of Action, Order and their interaction were not significant (F(1,19)=1.31, p>.05, F(1,19)=0.17, p>.05 and F(1,19)=1.79, p>.05, respectively). See figure 3.
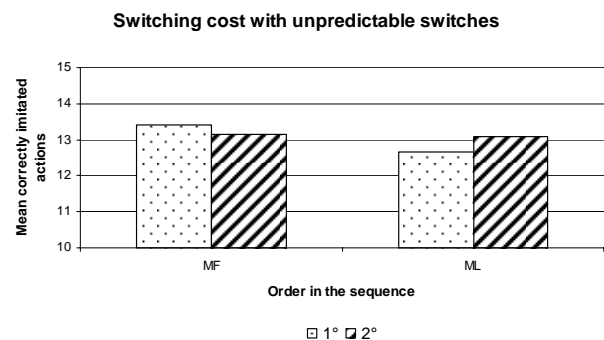
Switching cost with unpredictable switches

Figure 3: switching cost for meaningful (MF) and meaningless (ML) action in Experiment 2

Further analyses. A 3-way ANOVA with Type o f Action and Order as within-subjects factors and Experiment as between-subjects factor was also carried out. None of the factors was significant (all p>.05) but their triple interaction (F(,37)=6.47, p<.05): Imitation accuracy on the first meaningful trial was significantly lower in Experiment 1 than in Experiment 2 (mean=11.89 and mean=13.40 respectively).

Discussion. This experiment did not lead to any switching costs, suggesting that when healthy individuals are presented with unpredictable sequences of meaningful and meaningless actions they tend to privilege the use of the direct route for reproducing both types of actions as already demonstrated in previous studies (Tessari & Rumiati, 2004; Rumiati et al., 2005; Tessari et al., 2006; Tessari et al., 2007).

Conclusion

When time constraints are imposed in a predictable condition (i.e. the fixed list), where participants can apply the most suitable process to perform the imitation task, switching cost was obtained only when subjects switched to meaningful actions and no switching cost was observed when subjects had to switch to meaningless actions. This might indicate the need to suppress the dominant, semantic route when imitating meaningless actions (see Meuter & Allport, 1998 for a similar argument in language switching). Furthermore, we found no switch cost when switches were unpredictable, that is in the mixed list. One plausible explanation for this finding is that participants used the direct route from the beginning and stick to it throughout the experiment as already suggested by previous studies on both normal individuals (Tessari & Rumiati, 2004) and brain-damaged patients (Tessari et al., 2007).

We conclude that the semantic route seems to be the dominant process in adult individuals, and that the modulation of the two cognitive processes seems to be modulated in a bottom-up fashion being influenced by the composition of the list.

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