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Motor Planning and Imitation
(Automatic and strategic effects in human imitation)

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Automatic and strategic effects in human imitation

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Imitation is a very important ability that allows an agent to acquire efficiently a wide range of movements by observing a demonstrator performing them. The tendency to imitate has long been noted in normal and abnormal human behavior, and in the last decade there has also been an increase in the number studies of imitation in children, monkeys and great apes. In this chapter we will review some main issues related to imitation, including whether imitation is innate or is the outcome of a learning process, whether it is uniquely human or is shared with other primates, as well as the most prominent accounts that have been put forward to explain how it works. We will then summarize the results from different sets of experiments which we have interpreted within a dual-route model. Normally, individuals use the sublexical, direct route to imitate novel, meaningless (ML) gestures and the lexical–semantic, indirect route (and possibly the sublexical route) to reproduce meaningful (MF) actions that are already in one's repertoire. We will show how a reduction in cognitive resources, caused either by experimental manipulations with healthy participants or by brain damage, may end up affecting the route selection in imitation. In particular, when MF and ML actions are presented intermingled, participants selected the direct route because it is suitable for imitating both stimulus types. Moreover, in the new Experiments 1 and 2 we also demonstrated that the sublexical route is selected even when either ML (Experiment 1) or both ML and MF actions (Experiment 2) were presented for longer periods of time. Finally we will illustrate the cerebral correlates of imitation of different action types, derived from the lesion analysis of patients with a selective stimulus-specific apraxia, and from a positron emission tomography study with healthy participants performing an imitation task. Based on our results, we propose that imitation of MF and ML actions is supported by common as well by dedicated brain regions.

Imitation is an innate process that is not only human

The discoveries of Meltzoff and collaborators in developmental psychology have modified the view, generally accepted until then, that humans gradually learned to imitate during the first years of life. Meltzoff and Moore (1977) reported that 2–3-week-old infants were able to reproduce specific human gestures performed by the demonstrator, such as mouth opening, tongue protrusion, lip protrusion, and hand opening, suggesting that imitation was an innate ability. This interpretation was strengthened by the subsequent finding that infants can imitate gestures immediately after birth (Meltzoff and Moore, 1983, 1989). Other developmental studies with older children demonstrated that 3-year-olds are able to learn how to solve tool-use problems from imitation (Want and Harris, 2001), and that their imitation process is goal-directed (Bekkering *et al.*, 2000, for an extensive discussion of the goal-directed theory see later in this chapter).

In the last 10 years, several controlled studies with monkeys and great apes have used imitation as a tool for investigating continuities and discontinuities in the evolution of mind. Infant chimpanzees seem to imitate human facial gestures in the first week of life (Myowa, 1996; Bard and Russell, 1999; Myowa-Yamakoshi *et al.*, 2004), suggesting that in humans and chimpanzees neonatal imitation shares similar features both with respect to the type of gestures they perform, and to the time-window in which imitation is observed. But is imitation of facial gestures an evolutionary acquisition of apes and humans alone? According to Ferrari *et al.* (2006), who have recently reported that infant macaques imitate mouth gestures performed by humans on the first day of life, the answer is no. One difference between chimps and humans and the infant macaques studied by Ferrari *et al.* (2006) is that in the latter imitation is seen only in the first days of life. This difference can be explained by the fact that motor and cognitive development is faster in the macaques than in both humans and chimpanzees.

Imitation is forever

Different research lines converge to support the argument that imitation is a contagious and automatic process. Social psychologists reported that we tend to whisper or speak louder when others do, scratch our head upon seeing someone else do it, walk slower in presence of elderly individuals, and cycle faster after seeing a cycling race on TV (Dijksterhuis and Bargh, 2001). This automaticity has been argued to be the ‘social glue’ that favours cooperation and affiliation among humans (Lakin *et al.*, 2003).

Using a stimulus–response (S-R) compatibility paradigm, Brass *et al.* (2000, 2005) showed how, in humans, the tendency to imitate seems to persist well into adulthood. The key finding of these studies is that observed finger movements, relative to symbolic or spatial cue, have a stronger influence on pre-instructed finger movement execution, and that the influence is even stronger (shorter reaction times) when observed and executed finger movements are compatible (i.e. observed and executed lifting; observed and executed tapping) compared with the incompatible mapping (lifting observed → tapping executed, and vice versa). These findings demonstrate that movement observation influences movement execution even in a task in which the response is predefined, thus supporting the assumption that this effect is automatic. Although in their experiments participants were not instructed to intentionally imitate the observed movements, Brass and colleagues argued that imitation of actions is a special case of S-R compatibility.

There are pathological conditions that alter dramatically the tendency to imitate observed behaviors of others, for instance after brain damage. On the one hand, there are patients with frontal lesions, who suffer from imitation behavior (IB) (Lhermitte *et al.*, 1986;

De Renzi *et al.*, 1996). In this behavior, patients imitate the examiner's gestures, although they have not been instructed to do so and have even been discouraged. The authors proposed that IB is caused by impairment of the inhibitory action of the mediobasal frontal cortex on the parietal lobe, thereby realizing parietal lobe activity. In this context, the behavior the patients imitate is not novel but belongs already to their motor repertoire. Brass *et al.* (2005) have clarified that the inhibition of prepotent imitative and general overlearned responses (as in the Stroop-like tasks) entails different functional mechanisms. Except for a common area related to the generation of the stop signal, inhibition of overlearned responses involves a fronto-parietal network, whereas the inhibition of imitative responses is sustained by areas that require distinguishing between self-generated and externally triggered motor representations.

On the other hand, patients with ideomotor apraxia (in short IMA) exhibit the opposite pattern, i.e. a dramatic reduction of their ability to imitate actions, following lesions typically, though not exclusively, of the left hemisphere (De Renzi *et al.*, 1981), and in particular of the inferior posterior parietal cortex (e.g. Goldenberg and Hagmann, 1997; Buxbaum *et al.*, 2005). A faulty imitation is not the only symptom of IMA for patients may also be impaired when they gesture on verbal command (Merians *et al.*, 1997). However, given that IMA patients often suffer from co-occurring aphasia, it is preferred to test them using an imitation task to circumvent possible poor comprehension.

'Direct' models of imitation

Different accounts have been submitted to explain how imitation works, ranging from the direct-mapping approach (e.g. Prinz, 1997) on the one end, to the active intermodal mapping (AIM) (Meltzoff and Moore 1977, 1997), in an intermediate level, to the dual-route (Rothi *et al.*, 1991; Rumiati and Tessari, 2002; Tessari and Rumiati, 2004) and the goal-directed theory (Bekkering, Wohlschläger and colleagues) on the opposite end.

The central tenet of the direct-mapping approach, as elaborated by Prinz and colleagues (Prinz, 1997; Hommel *et al.*, 2001), is that observing the effect of an action facilitates its execution because perception and acton planning share a common representational code. Applying this concept to the brain, it follows that perception of an action activates the motor system directly. More specifically, it has been proposed that, in humans, the neural correlate of the direct mapping is the bilateral fronto-parietal mirror neuron system (MNS), engaged both in observation and execution of purposeful actions (e.g. Iacoboni *et al.*, 1999). The human direct matching–MNS seems to be tuned specifically to biological actions. Tai *et al.* (2004), for instance, showed that when participants observed manual grasping actions performed by a human model, a significant neural response was elicited in the left premotor cortex. This activation was not evident for the observation of grasping actions, performed by a robot model, commanded by an experimenter.

The key concept of the AIM hypothesis, developed Meltzoff and Moore (1977) to explain early facial imitation, is 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. This is achieved because the seen and performed acts are coded within a common framework which enables newborns to detect equivalences between their own acts and ones they see. In 1997, the same authors have fleshed out the AIM hypothesis by adding three new theoretical concepts (Meltzoff and Moore, 1997). First, infants relate parts of their own bodies to corresponding ones of the adult's by means of an 'organ identification'. For instance, the child who sees a tongue protrusion, initially moves the tongue slightly in the oral cavity, as if the infant isolates the part of the body to move before processing how to move it. Second, infants need to learn through 'body babbling' what muscle movements achieve a particular body configuration, such as tongue protrusion, very much in the same way they learn the articulatory–auditory relation through vocal babbling. Thanks to this experiential process, infants learn to map movements and the organ-relation end-states. Third, 'organ relations', such as 'tongue-to-lips', serve as the cross-modal equivalence underlying imitation: infants attempt to match the organ relations they see exhibited by the adults with those they feel themselves make. Meltzoff and Moore (1997) argue that important aspects of later social cognition are rooted in this initial cross-modal equivalence between self and other.

There are, however, some facts that cannot be easily accounted for by a theoretical approach that directs all its emphasis towards a direct input–output correspondence. For instance, when asked to copy movements to a right or left ear (the object), using either the ipsilateral or the contralateral hand (the agent), performing a movement parallel to the body or one crossing the body line (the movement paths), or crossing their arms (the salient feature), children tended to select either the object or the agent correctly, but neglected the movement paths and the salient feature (Bekkering *et al.*, 2000). If the mechanism underlying imitation were a direct matching, children should be able to imitate the action of the demonstrator as presented but they do not. By contrast, they seem to decompose the observed action into goals which can be the objects to which the actions are directed, the agents that perform actions, or the movement. Goals are hierarchically organized, with some of them being more important than others. The process of decomposing–recomposing the observed action depends critically on the cognitive resources available and this would explain why children, who have developmental limitations of their processing capacities, tend to reproduce the most relevant goals and ignore others. In Bekkering *et al.*'s (2000) study, objects and agents presumably were more important goals than movement paths.

In preverbal children, imitation of a goal-directed action seems to be an interpretative process rather than a simple re-enactment of the means used by the demonstrator (as in Meltzoff's view). Gergely *et al.* (2002) showed that 14-month-old infants imitated the action of lighting the lamp with the head in the condition in which the demonstrator had the hand occupied (pretending to be cold, she had a blanket wrapped around herself) relative to when the demonstrator had her hands free (69 versus 21%). Finally, it appears that healthy adults too interpret the seen actions in terms of goals hierarchically ordered and end up performing the most important goals at the expense of the less important ones (Wohlschläger *et al.*, 2003). This is achieved when the behavior to be imitated is made harder by increasing the number of potential goals.

Another set of findings not easily explained by the direct-mapping view relates to neuropsychology. There are patients with selective deficits for imitation of either ML or MF actions (Goldenberg and Hagmann, 1997; Peigneux *et al.*, 2000; Bartolo *et al.*, 2001). If there were a unique mechanism involved in imitation (i.e. direct matching), there should be no differences in imitation of different goals or types of movements.

In this chapter we will argue that a dual-process model for imitation can accommodate the latter findings better. One such model, analogous to those of language production (e.g. Patterson and Shevell, 1987), has been put forward first by Rothi *et al.* (1991), and subsequently modified by Goldenberg and Hagmann (1997), Cubelli *et al.* (2000), and Rumiati and colleagues (Rumiati and Tessari, 2002; Tessari and Rumiati, 2004; Rumiati *et al.*, 2005).

The dual-route model

Figure 23.1 reproduces a simplified and modified version of the model proposed by Rothi *et al.* (1991).

A key feature of this model is the presence of two distinct processing mechanisms for imitation: a sublexical, direct route for reproducing novel actions (but also those already known), and a lexical–semantic, indirect route for reproducing only overlearned actions. In this context, the term 'sublexical' refers to the conversion of the subunits in which

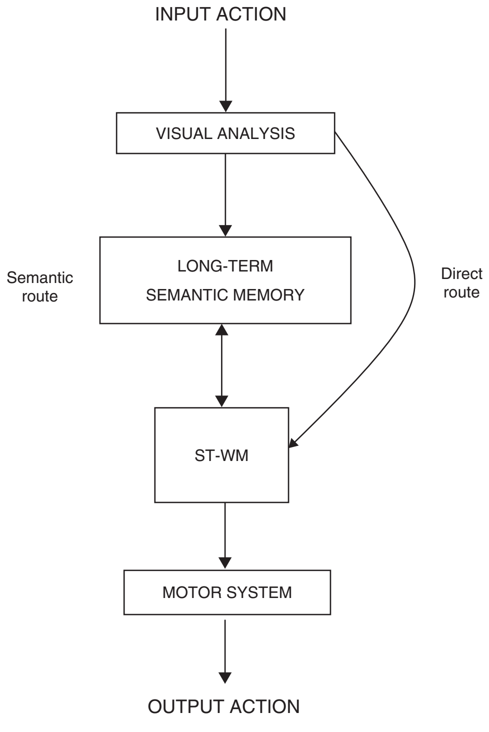

Figure 23.1 Two-route model of imitation from Tessari and Rumiati (2004). Following visual analysis, meaningful actions automatically activate the selection of the semantic long-term memory route. The sublexical, direct route is normally selected to imitate meaningless actions, but can also be used to reproduce both meaningful and meaningless actions when they are presented intermingled. ST/WM, short-term/working memory.

the seen action can be parsed, into a motor output, whilst the term 'lexical–semantic' refers to a process that applies to an action for which a lexical–semantic representation already exists.

Both known and novel actions are visually analyzed in a common stage; then, if the action to be imitated is already part of the repertoire of the person performing the imitation task, the action stimulus can be reproduced using the lexical–semantic route that comprises different processing stages, including the action input lexicon, the semantic system and the action output lexicon, before being held in a short-term/working-memory subsystem (see also Cubelli *et al.*, 2000, who refer to this latter processing stage as the 'buffer'). If, however, the action to be imitated is novel, then the subject has to use the sublexical, direct route, which allows the conversion of any input visually presented action into a motor output. The outcome of the visuo-motor transformation is then briefly kept in the short-term memory subsystem, a processing stage in common with the semantic route. At this point, known or novel actions held in memory can be generated by the imitators.

Observations of brain-damaged patients eventually provided support for some of the predictions derived from such a model. As far as imitation is concerned, four cases have so far been reported with selective imitation of ML actions (Goldenberg and Hagmann, 1997; Peigneux *et al.*, 2000; Bartolo *et al.*, 2001), and one with a selective imitation of MF actions (Bartolo *et al.*, 2001). In these studies, patients' ability to imitate has been assessed using separate lists of MF and ML actions so that they could, depending on the type of actions contained in the list, select either the sublexical or the lexical–semantic route, each of which could be damaged.

By contrast, in studies of large groups, patients showed no difference in their ability to imitate the two action types (De Renzi *et al.*, 1981; Cubelli *et al.*, 2000; Toraldo *et al.*, 2001). As patients were administered a test in which MF and ML actions were presented intermingled, they may have selected the sublexical route to perform the task because it allows imitation of both action types present in the list, and it reduces the costs of switching between processing routes. As this route was likely to be damaged in the patients examined, no difference in imitation of MF and ML actions was found.

Thus, the selection of the route that provides best imitation performance could depend not only on the type of action to be imitated (MF or ML) but also on other factors such as external (list) and internal (resources) conditions.

Evidence from healthy individuals

Tessari and Rumiati (2004) provided evidence in support of a dual-route model for action imitation by studying healthy participants. In three experiments, the authors imposed a deadline technique consisting of a fast presentation of the stimulus and a very limited time for the response. Tessari and Rumiati (2004) found that the deadline paradigm temporarily reduced the participants' abilities to imitate. To date, without time constraints, healthy observers imitate novel, ML and familiar, MF actions at ceiling, in either mixed or blocked conditions. The MF actions used in this study were pantomimes of object use, and the ML actions were similar in many respects to the MF ones except that they were not recognized. In Experiments 1 and 2, overall imitation was better with MF than with ML actions. More specifically, when ML and MF actions were presented in separate lists, participants selected the lexical–semantic route for MF actions and the sublexical route for ML actions, with MF actions being imitated better than ML actions (Experiments 1A and 2A). However, when MF and ML actions were presented intermingled, no difference in imitation of MF and ML actions was observed (Experiments 1B and 2B).

Tessari and Rumiati (2004) argued that participants selected the sublexical route in the mixed presentation (Experiments 1B, and 2B) and when there were more ML than MF actions in a list (Experiment 3B). Selecting the direct route allows imitation of both action types and reduces switching costs that would not easily be sustained by the subjects whose resources are limited by the deadline. Due to time constraints, healthy controls with reduced cognitive resources strategically select the imitation mechanism that is more convenient. Similar effects have been found in reading studies (e.g. Monsell *et al.*, 1992; Tabossi and Laghi, 1992): when nonwords were inserted in a list of words, readers used the sublexical route to read regular words as well as nonwords, instead of selecting the lexical route.

After training, ML actions can be imitated even better than MF actions, perhaps because they have only one representation in episodic, long-term memory and therefore there is no competition among alternative representations prior to action selection (Tessari *et al.*, 2006).

Testing the strategic control in the mixed condition

In the study by Tessari and Rumiati (2004), the failure to report a difference in performance when subjects executed the imitation task in the mixed condition has an alternative explanation. We argued that, in this condition, MF and ML actions were imitated to the same extent because subjects selected a strategy (i.e. the sublexical, direct route) that allowed them to imitate both action types and to avoid switching costs. However, the inclusion of ML among MF actions might have lowered the overall performance. In order to overcome the resource limits, the cognitive system may build up motor hierarchies with the subunits of which the motor input is constituted. This must be particularly true for ML actions, as they have no underlying concept that may glue the motor units together. These operations are likely to require a little more than 1 s, which was the overall time we allowed subjects to watch the action to be imitated (Tessari and Rumiati, 2004). Had they been allowed more time to process the ML input, subjects would have been able to parse and transform it into a coherent motor output. Moreover, having reduced the time pressure, at least at the input end, subjects would have also been in the best position to select the imitative process according to the nature of the stimulus, i.e. semantic for MF and direct for ML actions). This would lead to better imitation of MF relative to ML actions, as in the block presentation (see Tessari and Rumiati, 2004). To test this prediction, in Experiment 1 the presentation time of meaningless actions was increased in order to allow participants more time to visually analyze the ML actions. The ML actions used in this experiment were those from which the actions employed in Tessari and Rumiati (2004) had been ‘extracted’. In other words they were the same but more extended temporarily.

Experiment 1: Longer presentation times for meaningless actions only

Seventeen right-handed individuals, all students of the University of Trieste, participated in the study. They had either normal or corrected-to-normal vision. Their handedness was tested with the Edinburgh Inventory (Oldfield, 1971). Except for the duration time of the ML actions, everything else was as in Experiment 2B from Tessari and Rumiati (2004), including the fact that participants were informed that there were two stimulus types presented intermingled. Each trial started with either a MF action which lasted for 1 s, or a ML action which lasted 2 s, followed by a 0.5 s blank interval at the end of which a beep sounded for 0.25 s.

Results are plotted in Figure 23.2. A paired-sampled *t*-test was performed on the accuracy results. No significant effect of Type of Action emerged [$t(16) = 1.012$, not significant]: mean MF = 63.71, SD = 7.34; mean ML = 65.71, SD = 5.50.

Experiment 2: Longer presentation time for both meaningful and meaningless actions

Participants did not seem to have selected the two processes depending on the stimulus type, as predicted, even though they were presented with ML actions for a longer time period than in the previous mixed presentation experiments (Tessari and Rumiati, 2004), and were aware of this manipulation. In contrast, participants may have allocated attentional resources to detect longer trials, leaving few resources for switching between mechanisms. We therefore carried out Experiment 2, in which both MF and ML actions were presented for a longer time period. With this manipulation we aimed to prevent participants from using the presentation time as a cue for identifying the stimulus type, and to allow them to apply the imitation route according to the stimulus type (direct route for ML and semantic route for MF actions).

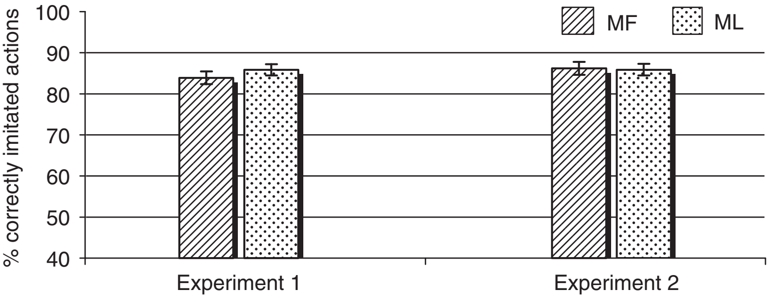

Figure 23.2 Percentages of correctly imitated meaningful (MF) and meaningless (ML) actions in Experiments 1 and 2 are plotted. Error bars represent standard errors.

Eighteen right-handed individuals, all students of the University of Trieste, participated in the study. They had either normal or corrected-to-normal vision. Their handedness was tested with the Edinburgh Inventory (Oldfield, 1971).

MF and ML actions, as well as the procedure were the same as in Experiment 1, except that both action types were now presented for 2 s. Both action types used in this experiment were those from which the actions employed in Tessari and Rumiati (2004) were extracted.

Correct responses were entered in a paired-sample *t*-test. No significant difference emerged between MF and ML actions [$t(17) = 1.45, P > 0.05$: mean MF = 66.37, SD = 5.74; mean ML = 68, SD = 4.81]. Results are plotted in Figure 23.2.

Further analysis

We compared the imitation performance in Experiments 1 and 2 of MF and ML actions, and found no difference for either type of action [independent sample *t*-test, $t(46) = 0.978$, $P > 0.05$, and $t(46) = 1.116$, $P > 0.05$, respectively]. In a second analysis, we compared Experiments 1 and 2 with Experiment 2B from Tessari and Rumiati (2004), and found a significant main effect of Experiment [$F(1,49) = 32.67$, $P < 0.001$]: performance in Experiment 2B was lower than that in Experiments 1 and 2 (mean Experiment 2B = 54.89, mean Experiments 1 and 2 = 68.36). The main effect of Type of Actions and the Experiment × Type of Actions interaction were not significant (all $P > 0.05$) (see Figure 23.3).

Discussion of Experiments 1 and 2

No significant difference emerged between imitation of MF and ML actions in either Experiment 1 or Experiment 2. Presenting ML actions (Experiment 1) or both ML and MF actions (Experiment 2) for a longer time than we did in a previous study (Tessari and Rumiati, 2004) does not seem to be sufficient for participants to switch between the two imitative processes. Compared with the results obtained in Experiment 2B (from Tessari and Rumiati, 2004), a decrease in processing demands on the cognitive system, made possible by the longer presentation time, improved overall subjects' performance in the

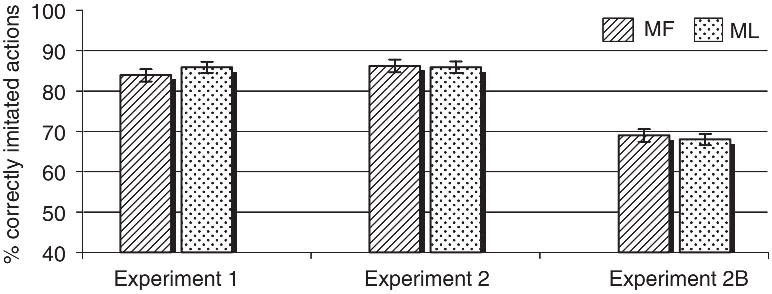

Figure 23.3 Percentages of correctly imitated meaningful (MF) and meaningless (ML) actions in Experiments 1, 2 and Experiment 2B (Tessari and Rumiati, 2004) are plotted. Error bars represent standard errors.

present Experiments 1 and 2, but it did not alter the strategy selection. The present results suggest that the lack of a difference in imitating MF and ML actions that we found in previous experiments in which the presentation was intermingled is unlikely to be due to ML actions lowering the overall performance.

Taken together, these studies suggest that, although there might be preferred mechanisms for imitating different action categories (the sublexical route for novel actions and the lexical–semantic route for familiar actions), there are circumstances in which the cognitive system overcomes this specialization. One such condition is offered by the mixed presentation. When it becomes apparent that there are new movements to be reproduced, mixed together with known ones, the sublexical route is selected because it permits us to imitate all possible movements. Here we presented a longer version of ML actions (Experiment 1) and MF and ML actions (Experiment 2) to free resources that in previous experiments (Tessari and Rumiati, 2004) might have been consumed in the attempt to process the visual input. Assuming that this interpretation is correct, we are tempted to conclude from the present results that the composition of the list is more critical and that resources may play an additional role when the imitation task is performed under time pressure and in brain-damaged patients.

Neuropsychological evidence

Brain-damaged patients, whose cognitive resources are reduced by the lesion, are expected to select the most convenient route for imitation according to the list composition, as healthy controls with limited time did (Tessari and Rumiati, 2004).

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In a recent study (Tessari *et al.*, in press), 32 patients with either left- or right-brain damage (LBD and RBD) and 20 healthy age-matched controls were asked to imitate the same MF ($n = 20$) and ML ($n = 20$) actions which were presented either in separated blocks or intermingled. The stimuli were the same as in Tessari and Rumiati (2004). Behavioral results were analyzed at the group level and at the single-patient level. As a group, patients performed the imitation task worse than controls. Irrespective of the lesion side they showed a better performance in the blocked than in the mixed condition. However, altogether LBD patients' performed worse than RBD patients. No significant correlations were found between action recognition, object use and action imitation of all patients, suggesting that these three abilities do not entirely share the same representations or computations (see Buxbaum *et al.*, 2005, for a different finding).

All patients in the study of Tessari *et al.* (in press) imitated MF and ML actions in the mixed presentation with the same accuracy. In contrast, eight patients showed a simple dissociation in imitation of MF and ML actions in the blocked presentation (see Figure 23.4).

The presence of single dissociations suggests that sublexical and lexical–semantic routes involved in processing MF and ML actions in the context of imitation might be independent. However, in the case of patients who showed only a *strong* dissociation (i.e. the performance on the task they do better on is worse than that of healthy controls), a damage to the second route cannot be excluded.

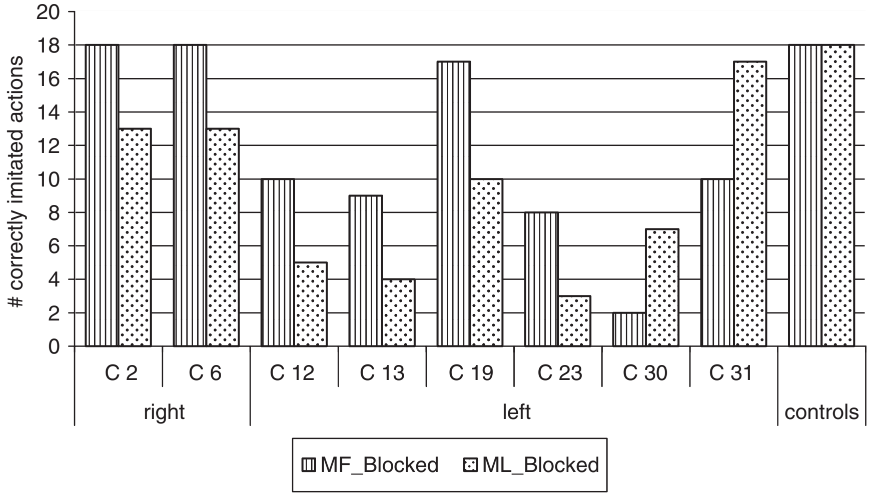

Figure 23.4 Performance of patients showing a dissociation in imitation of meaningful and meaningless actions in the blocked condition (see also Tessari *et al.* in press); 'right' refers to patients with right-brain damage and 'left' to patients with left-brain damage.

It is the *classical* dissociation (i.e. on the task on which patients are not impaired, they performed as well as healthy controls) in imitation of MF and ML actions shown by two patients (cases 19 and 31) that allows us to argue for a functional independency of the two routes. Case 19, who imitated MF better than ML actions is likely to have a damaged sublexical route, whereas case 31 who imitated ML better than MF actions is likely to have a damaged lexical–semantic route.

The brain structures lesioned in the LBD patients who imitated MF actions better than ML actions overlapped in the superior temporal lobe and the ventral portion of the angular gyrus; and those lesioned in the RBD patients with the same behavioral deficit overlapped in the basal ganglia. On the other hand, the two patients who imitated ML better than MF actions had lesions involving the lateral and dorsal portion of the hippocampus, extending to the bordering white matter, and the dorsal angular gyrus.

Cerebral correlates of the two-route model

Overall, imaging studies carried out so far suggest that human imitation is sustained by a network of brain regions that include the inferior frontal gyrus, the dorsal and ventral premotor cortex, the inferior and the superior parietal cortex, and the posterior superior temporal cortex (see Brass and Heyes, 2005, for a review). To date, these areas have also been found activated during action perception.

Surprisingly few studies have investigated the cerebral correlates of the different processing mechanisms that may be involved in actual imitation. One such study is that performed by Peigneux *et al.* (2004) who, using positron emission tomography (PET), scanned subjects carrying out different tasks, including pantomime to command, imitation of novel and familiar gestures, and a functional–semantic association task. Among many interesting results, Peigneux *et al.* (2004) found that when imitation of familiar (either symbolic or non symbolic) gestures was associated with activations in the left angular and middle frontal gyri, and the right supramarginal gyrus and inferior parietal lobule; whereas imitation of novel, ML gestures was associated with inferior and superior parietal lobes bilaterally.

In a further imaging study, Grèzes *et al.* (1999) required subjects to observe novel ML actions with or without the purpose of imitating them, in addition to observing stationary hands as a baseline. These authors showed that, irrespective of the subjects' intentions, the activations of some brain areas changed depending on the level of the subjects' familiarization with the perceived ML actions. In particular, as subjects became more familiar with ML, a reduction of the neural activity in the motion-related areas in the dorsal stream was observed, as well as an increase in activation within the inferior parietal and frontopolar cortices.

The issue of dedicated cerebral correlates for imitation of MF and ML actions was explored by Rumiati *et al.* (2005) in 10 healthy individuals (mean age = 26, SD = 1.9) using PET. Thirty MF and 30 ML actions were used to create the lists to be presented in five experimental conditions of a parametric design (100% MF–0% ML; 70% MF–30% ML; 50% MF–50% ML; 30% MF–70% ML; 0% MF–100% ML), and in the baseline condition (observation of mixed 50% MF and 50 per cent ML actions). Imaging data were analyzed using SPM 99. Actions were comparable to those used in Tessari and Rumiati (2004) and in Tessari *et al.* (in press).

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Three sets of analyses were carried out. First, relative to action observation (baseline), imitation of either MF or ML actions seems to be sustained by a network of brain regions including: the left primary sensorimotor cortex, the left supplementary motor area, the ventral premotor cortex, the primary visual cortex, the parieto-occipital junction bilaterally, the left insular cortex, the left thalamus and the right cerebellum. The second set comprises two correlations. During imitation, a significant positive correlation ($P < 0.05$, corrected) of regional cerebral blood flow with the number of MF actions was observed in the left inferior temporal gyrus only; in contrast, a significant positive correlation ($P < 0.05$, corrected) with the amount of ML movements was observed in the right parieto-occipital junction.

The third set of analyses includes two direct categorical comparisons. Imitating MF (100%) relative to ML (100%) actions showed differential increases in neural activity ($P < 0.001$, uncorrected) in the left inferior temporal gyrus, the left parahippocampal gyrus, and the left angular gyrus. In contrast, imitating ML (100%) relative to MF (100%) actions revealed differential increases in neural activity ($P < 0.001$, uncorrected) in the superior parietal cortex bilaterally, in the right parieto-occipital junction, in the right occipito-temporal junction (MT, V5), and in the left superior temporal gyrus. Increased neural activity, common to imitation of ML and MF actions, relative to action observation was observed in a network of areas known to be involved in imitation of actions including primary sensorimotor cortex, supplementary motor area, and ventral premotor cortex.

Conclusions

The studies reviewed in this chapter hopefully demonstrate that the two-route model can accommodate data from healthy and brain-damaged patients. It can account for stimulus-specific deficits shown by patients, and it can explain the strategic control exerted by individuals with reduced cognitive abilities on route selection. The ability to strategically select the most appropriate mechanism might be a general feature of the brain as was found also in cognitive domains other than action.

Taken together, all these studies suggest that the lexical–semantic and sublexical mechanisms underlie action imitation, and, in addition to having in common some neural processes, also draw upon differential neural mechanisms.

In conclusion, a theory of *how* imitation is accomplished should include processes dealing with action at input or at output, but should also consider the role of intermediate representational levels of actions and that of a strategic control.

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